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VERTEBRATE PALEONTOLOGY

BY

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IN HARVARD UNIVERSITY

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PREFACE TO THE SECOND EDITION

THE decade of the 1930's was the most productive period in the history of vertebrate paleontology. Many new discoveries were made; more important, however, is the fact that research on both these new materials and on older types was pursued in a much more intensive fashion than ever before. Our views of vertebrate evolution have broadened in scope and deepened in perspective. As a result, the original text of this volume had gradually become outmoded and inadequate in many respects, and I was glad when the publishers suggested that the work be revised.

Certain general and introductory sections and those on groups in which advances in knowledge have been relatively small remain much as before although with minor changes throughout; about half the text, however, has been re-written. Three chapters have been added, presenting a summary of vertebrate faunal history, and the previously short systematic appendix has been expanded into the form of a comprehensive list of fossil genera. The illustrations remain much as in the first edition, although a number have been revised or replaced and a modest number of new figures have been added.

I am indebted to a considerable number of friends and colleagues for aid and advice. Dr. W. K. Gregory, who had already aided greatly in the preparation of the original text, has read and criticized much of the discussion of fishes in the present edition. Dr. D. H. Dunkle has aided in the classification of the arthrodires and discussion of other early fishes. Dr. T. S. Westoll has offered valuable criticisms of the account of the bony fishes and has aided greatly in the arrangement of the lower actinopterygians. I am indebted to Drs. H. B. Bigelow and W. C. Schroeder for access to the manuscript of their forthcoming work on sharks and to the former for profitable discussions of shark classification. Dr. L. R. David criticized helpfully the data on teleosts; I wish to emphasize that she is not responsible for the use here of a classification of teleosts differing in some respects from that followed by many American ichthyologists. Dr. J. T. Gregory allowed me the use of the manuscript of his work on *Trilophosaurus*, and Drs. E. C. Case and E. H. Sellards were kind enough to forward data regarding this reptile; in addition, the latter supplied me with a print of Dr. Sawin's restoration of *Buettneria*. Dr. R. S. Lull has criticized the account of the dinosaurs, and Mr. K. P. Schmidt has aided in the systematics of the "modern" reptile orders. I have profited by a discussion of reptile phylogeny with Dr. C. L. Camp. Dr. L. H. Miller has read the material dealing with birds.

I had hoped to profit again from Dr. G. G. Simpson's criticism of the mammal chapters. This was impossible, owing to his engagement in the military services; a partial recompense lay in his giving me access to the manuscript of his new work on the classification of mammals, which afforded a number of stimulating suggestions. I availed myself of the opportunity to check numerous genera, as I had compiled them, against his lists, particularly in the case of various Paleocene and South American forms, and I have adopted almost entirely his welcome simplification of proboscidean taxonomy. Dr. R. A. Stirton has made a number of helpful criticisms of the mammalian chapters and made available to me his unpublished work on palaeomerycids. Dr. V. L. VanderHoof read the sections on carnivores and sirenians. I am grateful to Dr. E. H. Colbert for criticism of the chapter on the Cenozoic and for interesting discussions on the evolution of artiodactyls. Dr. R. Kellogg aided in revision of the chapter on whales.

Dr. P. E. Raymond offered helpful criticisms of the earlier text. Dr. Tilly Edinger read and criticized much of the text. Throughout the preparation of the work I have been greatly and constantly aided by Miss Nelda E. Wright.

ALFRED SHERWOOD ROMER

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CHAPTER 1

INTRODUCTORY

THE present work gives a brief account of the history of vertebrates as revealed in the fossil record. We shall find it difficult, however, to confine ourselves strictly to fossil animals, for our subject is intimately related to many other scientific fields.

Vertebrate paleontology is essentially a biological science. To the paleontologist the animals of the present constitute but a brief cross-section of the vertebrate story. To him a separation of fossils from the modern forms which have descended from extinct types and are destined to become the fossils of the future would seem extremely artificial. Paleontology has much to learn from many other biological fields and much to give in return. With anatomy and evolutionary studies the connections are particularly close, while not only the taxonomist and ecologist but even workers in such seemingly remote fields as physiology and medicine may benefit from the possession of a historical background.

Paleontology is also intimately connected with the history of the earth itself, the field of historical geology. In the study of fossil human types the field of the vertebrate paleontologist overlaps that of the anthropologist. And, finally, the study of vertebrate evolution is history of a sort—but a history written in terms of millions of years rather than decades or centuries.

Since it is probable that this book will fall into the hands of readers with varied backgrounds, this opening chapter is devoted to a number of topics which may well be omitted by those grounded in the fundamentals of biology.

Vertebrate fossils.—But few of the countless individual animals of the past have been preserved to us as fossils. When a land animal dies today, its remains are usually scattered and destroyed by flesh-eaters or disintegrated by plant roots, soil acids, and bacterial action. Similar conditions, no doubt, were present in the past.

More exceptionally and more fortunately, a dead animal may be buried deep in a deposit of mud or sand, where the soft parts will usually quickly rot away but where the skeleton will be left surrounded by a gradually hardening matrix. The bony matter may persist and become gradually altered into a complex type of mineral in which much of the original constituents of the bone remain. Meanwhile, the cavities are, in the course of time, filled by minerals brought in in solution, so that the originally porous bone becomes a heavy, solid structure. But since the mineral matter filling the cavities is usually of a different nature from that into which the substance of the bone has been transformed, fossil bones, when sectioned and studied microscopically, usually show in perfect fashion the structural details of the original.

The softer portions of the body are sometimes, although much more rarely, preserved. Certain forms recently extinct, such as the dodo or the giant moas of New Zealand, may be considered as fossils of a sort, although their bones are usually but little altered chemically; in these cases feathers, ligaments, and other soft parts have been preserved. In America gigantic ground sloths are entirely extinct, and many of their remains are perfectly orthodox fossils; but in several instances skeletons have been found with patches of skin and hair still adherent. Extinct mammoths have been completely preserved in natural "cold storage" in the Siberian tundras, while woolly rhinoceroses have been found pickled in entirety in a waxy material from a Galician oil seep.

But even among much more ancient forms traces of soft parts are occasionally found. Specimens crushed flat in shales have in many cases preserved the outline of the skin. Certain dinosaurs appear to have been mummified before burial, so that the surrounding material, hardening before the disintegration of the skin, has left a cast of the mummy. In Bavarian lithographic limestone deposits, impressions are sometimes preserved of such delicate structures as feathers. In some small ancient amphibians the outlines of the stomach and intestine are visible; while in specimens of a Devonian shark, remains of the muscles are so perfectly preserved that individual fibers and their cross-striations are seen under the microscope.

We may gain much information concerning fossil forms in other ways. Footprints are often found in the now solidified mud flats of former periods. Eggshells pertaining to various groups—birds, turtles, skates, dinosaurs—have been discovered; and series of growth stages are known in some forms. Much information can be gathered concerning the food habits of extinct animals, aside from the knowledge afforded by the teeth and skeleton. Remains of the bones of devoured animals have been found in the position of the stomach; "gizzard stones" have been discovered lying within the skeletons of several reptilian types. Tooth marks tell us of the fate of the animal whose bones bear them. Feces, the remains of digestion, known as coprolites in the fossil state, are frequently encountered. Wounds and diseased conditions may be discerned on the bones of fossils. Even though actual remains of such structures as blood vessels, nerves, brains, and muscles are almost never found, a study of the skeleton gives us much information concerning them.

Evolutionary theories and phenomena.—In considering many curious and widely divergent animals adapted to a great variety of modes of life, it is impossible to avoid speculation as to the processes through which their evolutionary development was accomplished. This subject cannot be adequately discussed here, but we shall mention a few of the chief problems involved and the theories brought forward for their solution.

All animals are well fitted for the lives they lead (although sometimes, it is true, the fit does not seem to be a perfect one). We also find, in almost every case where fossil ancestors are known, that these animals have descended with many modifications in structure from forms seemingly less well adapted to their present modes of life. How have these changes come about?

Occasionally we find a statement of this type: "The giraffe, descended from short-necked ancestors, has acquired a long neck because it is useful to him in browsing off the higher branches of the trees." It is true that the long neck is of use to the giraffe, but the citation of a useful result does not in itself explain the nature of the process by which the result was obtained. The statement given would suggest either that some power outside the giraffe brought about the change with a useful end in view or that the giraffe had thought the matter over and brought about the change through his own volition. The first suggestion immediately takes us outside the realm of scientific thought; the second seems obviously absurd, although certain theorists have suggested the existence of some vague "vital force," a mysterious inner "urge," which has driven animals on toward an evolutionary goal.

A much more plausible suggestion is that which may be applied under the theory of the inheritance of acquired characters, or the effect of the use and disuse of parts, advocated more than a century ago by the French naturalist, Lamarck. It might be that the individual giraffe, by constantly stretching after the foliage on the higher branches, tended to increase the length of his neck during life and that this increase was transmitted to his offspring; a cumulation of such individual lengthenings was supposed to have resulted in the development of a long-necked from a short-necked form. This type of theory is plausible at first sight; but there is no evidence, despite repeated experiments, that changes taking place in the body of an individual during his lifetime produce any similar effect in his offspring.

A much sounder theory to explain evolutionary changes, and one which first brought about general belief in evolution, was that advocated by Darwin three-quarters of a century ago. The Darwinian theory points out that no two animals are exactly alike and that, to cite the giraffe again, a form with a neck slightly longer than the average would, especially in times of famine, have a better chance of survival than a shorter-necked form. This selective process would tend, Darwin believed, to the gradual development of the long neck.

Darwin assumed the presence in nature of individual variations which were inherited. Modern experimental work has done much to clear up this situation. It is now known that many individual differences are due to the influence of the environment and are not passed on to descendants and that most other individual characters do not mark the appearance of new features but are merely the result of varied combinations of characters already present in the species. Under such circumstances, all selection could do would be to sort out the best of the existing factors. Beyond this the evolutionary process could not go, were it not that occasionally there occur mutations—definite changes in the germ cells which give rise to the next generation—produced seemingly without relation to the needs of the animal and making definite, although usually small, changes in the structure of the descendants. Though mainly injurious and hence quickly weeded out, an occasional favorable mutation would offer new material for the selective process to work upon; a "chance" mutation increasing the length of a giraffe's neck without other unfavorable accompanying features might tend to be bred into the race. Such an evolutionary process would obviously be slow in action. But even such a comparatively modern animal as a giraffe has had millions of years at its disposal.

In many groups of fossils it would seem that there has been no such "indecision" as the theory just outlined would suggest; groups once started along an evolutionary line have seemingly kept straight on toward a "goal" without deviation. Because of this, there has been built up a theory of orthogenesis, or "straight-line" evolution. But the apparent absence of side branches may be due to the fact that they were nipped in the bud; selection alone might have resulted in an advance in the single direction of greatest adaptive value. Much seeming orthogenesis may thus be explained through mutation and selection. There are still, however, many puzzling facts; and we are far from a complete and satisfactory solution to all of our problems of vertebrate evolution.

Both living and extinct vertebrates show many cases of wide evolutionary divergence within a group, parallel evolutionary tendencies in related forms, and close convergence in adaptive features in unrelated types. Competition within an animal group encourages divergent adaptations toward varied modes of life and produces an adaptive radiation. A striking example is the radiation of the Australian marsupials, which presumably began at the dawn of the Tertiary. The kangaroo and the Tasmanian wolf are unlike in all adaptive characters; but basically both are clearly derivable from a primitive type not unlike the opossum and are members of the same order.

The adaptive radiation of a number of groups tends to result in convergence in evolution—the attainment of similar adaptations by two or more unrelated types. The Tasmanian wolf is similar in many features to the true wolves of other continents; the pouched Australian wombat is similar to a woodchuck. But these resemblances do not at all imply relationships; they are merely the taking-on of similar structural features necessary for survival in similar modes of life.

A very different phenomenon is that of parallelism—the tendency for two or more closely related types to undergo similar structural changes. Several types of extinct South African mammal-like reptiles had a secondary palate like that of mammals. We are sure that this feature was not present in their common ancestor but that, with a similar ancestry and similar build, there has been a tendency for related forms to acquire similar structures—to "drift" in the same evolutionary direction.

Taxonomy and classification.—Zoölogists have found it necessary, in referring to living animals, to use a system of scientific names formed mainly from Greek and Latin roots, rather than variable popular terms. This necessity is even greater in the case of extinct forms for which no popular names can well exist. Every animal bears a double name: the first, that of a genus, usually including a number of related forms; the second, that of the particular species of that group to which reference is made. Thus the domestic dog, together with the wolves and jackals, constitute the genus *Canis.* When referring to the dog, the specific name is added—*Canis familiaris;* the wolf, a close relative, is *Canis lupus.* This system is not unlike our human usage of proper names and surnames, only the order is reversed.

Upon the genus and species as a base has been erected a system of classification originally designed as a method of "pigeonholing" animals in larger and smaller groups according to the degree of resemblance between them. Thus, for example, the dogs are obviously fairly closely related to the foxes and to other doglike tropical forms; and these are all united in a family, the Canidae. This group, in turn, is somewhat more distantly related to the cats, bears, and other flesh-eaters; and all these forms are united in an order, the Carnivora. This great group, again, has many features (such as the nursing of young and the presence of hair) which tend to bind it with an array of forms ranging from men to bats and whales; all these are considered members of a common class, the Mammalia. These mammals have a number of characters (such as the possession of an internal skeleton) also present in birds, reptiles, amphibians, and fishes; and, in consequence, all are grouped together in a phylum, the Chordata, one of the primary subdivisions of the animal kingdom. The complete list of major terms used in such a classification is thus: phylum, class, order, family, genus, and species. Further flexibility is often obtained by using prefixes to give such terms as subclass and superorder.

Originally adopted merely as a convenient method of "sorting out" animals, classification was put in a new light by the recognition of the evolutionary theory. Obviously these various taxonomic divisions represented, in a general way, the branches of the family tree. There has been a continual attempt to make classifications "natural," to see that each group established —whether genus, family, or higher division—should contain only forms descended from a common ancestor.

With living types alone to consider, groups may be fairly easily established and defined. But with the continued discovery of intermediate fossil types, classification becomes increasingly difficult. The living Equidae (horses, asses, and zebras) can be easily distinguished from the related rhinoceroses by such characters as the presence of but a single toe on each foot and the absence of horns. But some of the earliest horses had three toes, as do the rhinoceroses; and many of the early rhinoceroses were hornless. We cannot always give definitions which will hold true of all members of a group; we can merely cite the characters of typical members and build the groups about them. Tendencies, rather than the arrival at specific conditions, must be our criteria. Only a few late horses are actually one-toed, but a trend in that direction was early evident; the ancestral rhinoceroses were hornless, but a tendency for the development of horns soon appeared in several independent lines.

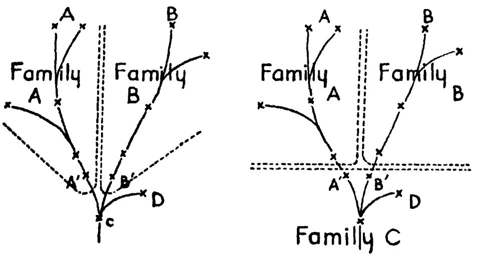


FIG. 1.—Diagram to show the contrast between "vertical" and "horizontal" classifications. A hypothetical family tree showing the descent of two living forms, *A* and *B* (horses and rhinoceroses, for example) from a common ancestral form, *C;* known forms are indicated by crosses. At the left, a vertical classification; the divisions between groups are carried as far down to the roots as possible. This makes clear the relation of early ancestors (*A′ B′*) to their descendants but separates them sharply from *C*, the common ancestor, and other side branches, such as *D*, to which they are closely related. At the right, a "horizontal" classification, which unites all the similar early forms into a common ancestral group, *C*, but obscures the relationship of *A′* and *B′* to their descendants.

Two types of classification are possible—"vertical" and "horizontal" (Fig. 1). Under the first system each family or other unit comprises all members of a known line from its first beginnings to its end or to modern times; the cleavage between lines is carried down to the very base of the evolutionary tree. But when, for example, forms are discovered seemingly ancestral to two distinct families or closely related to both their inclusion in one or the other seems improper. Under such circumstances the best solution seems to be a "horizontal" cleavage, the erection of a stem group, including the base from which the long-lived later families have been derived.

The large number of taxonomic terms with which one must become familiar in the study of fossil vertebrates tends to dishearten the beginner. But it will soon be recognized that (except in cases where names of persons or localities have been utilized) these terms are mainly compounded from but a few-score simple and easily recognizable Greek and Latin roots and are based on some real or fancied characteristic of the form described.

It is to be noted that, while considerable variation occurs in the formation of names of various larger groups, those of superfamilies usually end in *-oidea*, those of families invariably end in *-idae*, of subfamilies in *-inae*, all suffixed to the root of the name of a typical included genus, as Equoidea, horse-like forms; Equidae, horses; Equinae, modern horses; *Equus*, horse genus.

Vertebrate structure.—Before we can adequately discuss the history of the varied vertebrate types, a basic knowledge of their anatomy is a necessity. We shall here briefly review some of the more essential structures of the primitive water-living vertebrates, the fishes, especially as regards the skeletal system. (The morphological features of higher vertebrates will be discussed later.)

All vertebrates are bilaterally symmetrical animals, with the long axis of the body usually in a horizontal position and with a tendency for the concentration of organs related to the environment at the anterior end. This type of symmetry appears to be an expression of the usually active life of vertebrates, as contrasted with the comparative immobility of those invertebrates possessing radial symmetry. In land animals the development of large limbs tends somewhat to mask the primitively simple arrangement, while a radical change in the position of the body axis occurs in man and other bipeds.

Body form in fishes.—The ideal shape for a swimming vertebrate is that which engineers have approached in torpedoes and ship hulls as offering least resistance to the water—streamlined, with the maximum girth somewhat anterior to the middle. Actively swimming fish usually have this shape. Locomotion in such forms is principally accomplished by lateral undulations of the trunk and tail, a series of curves traveling backward and pushing the fish forward through the water; paired fins are usually steering organs only. Sinuosity is sometimes exaggerated, giving eel-like forms, usually degenerate end-products of evolutionary lines; while bottom-living types are usually depressed, with broad flat bodies.

Lying dorsally and ventrally along the main axis of the fish body are unpaired median fins consisting of a dorsal fin or fins projecting from the upper side of the body; a caudal fin, in the tail region; and an anal fin, lying behind the anus (Fig. 2). Dorsal fins are usually one or two in number in primitive types; a single anal fin is common. There may be great variation in the way of fusion or subdivision of the dorsal fins and fusion of either anal or dorsals with the caudal.

Two types of caudal fin are common in more primitive fish—the diphycercal and the heterocercal (Fig. 3). In the former the fleshy termination of the body containing the backbone runs straight out to the tip of the tail, and the fin is arranged symmetrically above and below it. In the heterocercal tail the body, containing the backbone, tips up posteriorly, and nearly all the development of the fin takes place beneath. In a few primitive fishes we find a reversal of this symmetry, the tip of the body tilting down and the fin erected above it—a reversed heterocercal type. The symmetrical diphycercal fin would seem logically to be the primitive type; the heterocercal, a specialized derivative. However, as we shall see, the latter is almost universal in the earliest members of most fish groups; and it is not improbable that the diphycercal type is in reality derived from this.

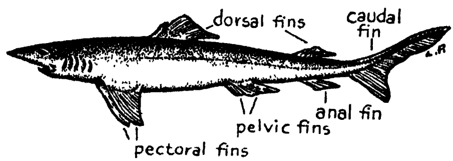


FIG. 2.—Diagram to show the position of the median and paired fins of fishes.

Notochord.—Vertebrates and their close relatives differ from the common invertebrate types in the possession of an internal skeleton for support and the facilitation of muscular movement. Among invertebrate types the skeleton, when present, is an external one, covering the surface of the body. Such a skeleton was early developed by vertebrates and is present in many forms today, but some internal skeletal structures are always present in addition. Most primitive and earliest of such internal structures, we believe, was the notochord—a long, slim rod usually extending from the base of the skull down the back to the tail. Composed of a soft, jelly-like material surrounded by a tough sheath, it forms in primitive vertebrates a firm but flexible supporting structure. In some water-living vertebrates it may persist throughout life; in higher types it is supplanted by the backbone but is always present in the embryo. Containing no hard parts, it is never preserved as a fossil.

Cartilage and bone.—In addition to the notochord, all vertebrates have a skeletal system composed of cartilage or bone. The former is a comparatively soft and translucent material, containing rounded cells and capable of growth by expansion. Ordinary cartilage is seldom preserved in fossil specimens, for it shrivels up and disintegrates easily upon exposure. In many fishes, however, calcium salts are laid down in the cartilage; and in this calcified condition it is a much firmer substance, capable of preservation.

Bone is, in microscopic section, easily distinguishable from cartilage by the presence of irregularly branching cell spaces, the presence of larger cavities for blood vessels which penetrate it, and its frequent arrangement in layers of deposition. It consists of a fibrous matrix heavily impregnated with calcium salts and forming a much stronger supporting material than cartilage. Unlike that substance, bone is incapable of expansion and can grow only by the addition of layers on its surface. In large bones the interior often contains a large marrow cavity as well as numerous smaller canals containing blood vessels and nerves.

Cartilage is almost never found in the skin but, when present, is confined to the deeper layers of the body. In existing lower vertebrates (cyclostomes and sharklike fishes), cartilage alone is present in the main portion of the skeleton; hence these forms lack any superficial skeletal covering except for small toothlike structures (dermal denticles) found in the skin of sharks, and spines, occasionally present in these fishes.

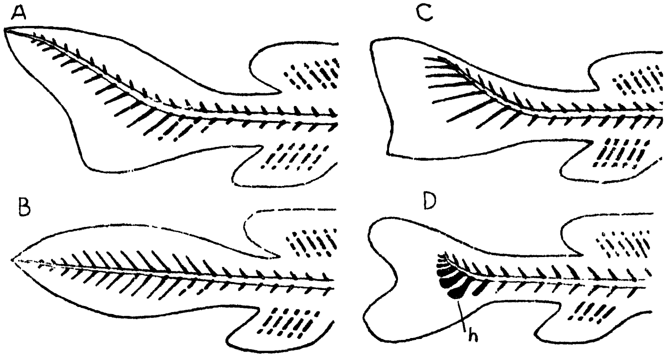


FIG. 3.—Diagram of caudal-fin types. *A*, Heterocercal type, found in most sharks, primitive lungfish, and actinopterygians and some early crossopterygians; *B*, diphycercal type, found in pleuracanth sharks and later lungfish and crossopterygians; *C*, abbreviated heterocercal and *D*, the derived homocercal type, found in later actinopterygians. In *D* the enlarged haemal arches (*h*) are termed "hypurals." *C* and *D* are undoubtedly derived from *A*, and so probably is *B* as well. (Modified from Goodrich, *Vertebrata Craniata.*)

In the higher groups of vertebrates, bone is the predominating skeletal material; little cartilage remains in the adult. Two categories of bone may be distinguished. The deeper portions of the skeleton are formed in the embryo in cartilage, just as in a shark or lamprey. As development proceeds, however, this cartilage is gradually destroyed and replaced by bone. Bone so formed is called "endochondral" or "cartilage-replacement" bone. Quite different in origin and development are dermal or membrane bones. These are never preceded in the embryo by cartilage and are, in contrast, superficial in origin, formed in the deeper layers of the skin. In fossil lower vertebrates dermal bones often covered the body completely, commonly as large plates over the head and shoulder region and smaller scales over the trunk and tail. The dermal plates often tend to unite with replacement bones, especially in the head region; the human skull, for example, is a composite of bones having these different origins.

In dermal bones and scales the deeper layers usually consist of characteristic bone, arranged in laminae; the middle portion in fishes presents a spongy appearance due to the presence of numerous blood vessels. The superficial layers vary greatly. Usually, however, bone cells are absent, and the material is a hard, compact tissue more or less comparable to the dentine which forms the main bulk of the teeth. The surface of fish scales and head plates is frequently finished by a layer of hard, shiny enamel, or enamel-like material, such as covers the teeth. Frequently the surface of the bony plates and scales of fishes shows an ornamentation of tubercles or ridges of dentine and enamel. These superficial structures seem comparable to the dermal denticles which are found in the skin of sharks and to the teeth which are present in jawed vertebrates. The spines often present on the fins of lower fish groups are characteristically formed of dentine and enamel, or similar materials.

Since the lowest of existing vertebrates are boneless, it has been, in the past, generally believed that the ancestral vertebrates were likewise cartilaginous forms and that the evolution of bone took place at a later stage in fish history. The presence of cartilage in the embryos of vertebrates which later acquired a bony skeleton was supposed to be a recapitulation of the phylogenetic history. But, as will be seen, all the oldest-known fishes possessed bone; many groups show a decrease rather than an increase in the degree of ossification in their skeletons as we pass from older to younger members; sharks and other cartilaginous fishes appear relatively late in the fossil record. It thus appears probable that vertebrates acquired bone at a very early stage in their history, although cartilage (with the useful power of growth by expansion) may have been present throughout as an embryonic type of structure. Cartilaginous vertebrates are thus reasonably regarded as degenerate forms which fail to mature in skeletal development and exhibit as adults an immature cartilaginous condition of the skeleton.

The internal skeletal structures of fishes may be grouped under four heads: the axial skeleton of the trunk and tail, the braincase, the branchial arch system, and the skeleton of the paired appendages.

Axial skeleton.—The main elements of the axial system are the vertebrae constituting the backbone. In some primitive forms the notochord remains large, but in most cases its growth is restricted, and in advanced types it disappears altogether in the adult. It is replaced by a series of vertebral centra of cartilage or bone. In some types the centra are formed by skeletal materials laid down as a thick sheath of tissue surrounding the notochord. In others they are formed from paired blocks of cartilage which occur on either side of the notochord and may unite to form ring-shaped centra (Fig. 4). Sometimes there are two such sets of cartilage blocks in a single body segment, and a double set of centra may result (cf. Fig. 94).

The nerve cord lies directly above the notochord; a ʎ-shaped protecting element usually develops above the centrum in each segment. The two branches—the neural arch—meet above the nerve cord and project upward as a neural spine. Important blood vessels lie just below the notochord in the tail, and these are usually surrounded by haemal arches, or chevron bones, analogous to the neural arches above.

In many specimens of Paleozoic and Mesozoic fishes, neural and haemal arches and ribs are present as bony or calcified structures, but the position of the centra shows only a blank space (cf. Figs. 28, 47, 71, 77, 80, etc.). Presumably, centra were present but tended to remain in a cartilaginous condition.

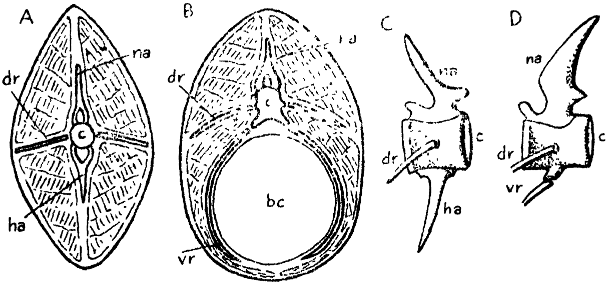


Fig. 4.—*A*, Diagrammatic section through the tail of a fish; *B*, section through the trunk, to show the relation of the vertebrae and ribs to the musculature and body cavity; *C*, diagrammatic caudal vertebra of a teleostean fish; *D*, trunk vertebra. Abbreviations: *bc*, body cavity; *c*, centrum; *dr*, dorsal ribs lying between dorsal and ventral muscle groups; *ha*, haemal arch and spine; *na*, neural arch and spine; *vr*, ventral ribs surrounding the body cavity.

Ribs extending out from the sides of the vertebrae and lying between dorsal and ventral groups of muscles are usually present in the trunk region; primitively they are present in every segment from the neck to the base of the tail. In addition to these intermuscular dorsal ribs, which are the only ones present in land forms, fish usually possess a second series—ventral ribs—which lie deeper and partially surround the body cavity. In the tail the ventral ribs are continued by the haemal arches.

Accessory skeletal structures are often found in the trunk. Additional bones are sometimes placed between various muscles (the shad is all too good an example), and in most land forms there is a breastbone, or sternum, to which many of the ribs attach ventrally. The median fins are supported by a series of parallel rodlike cartilages or bones—the radials; while below them, in the fish's body, basal elements connect them with the vertebral column. (In addition they are covered superficially and stiffened distally by scales or elongated rays derived from scales or from the skin itself.)

Appendicular skeleton.—Paired appendages—the paired fins of fishes and the homologous legs of land forms—are present in most vertebrates. There are normally two pairs (Fig. 2)—pectoral appendages just behind the gill region or neck and pelvic limbs typically situated at the posterior end of the trunk in front of the anal opening. Support for the limbs is afforded by girdles contained in the body of the animal. They are composed primarily of cartilage or of replacement bone, but the pectoral girdle often has membrane bones attached to its outer and anterior margins. Running out from the side of the girdle region is the appendage proper, the skeleton of which usually consists of a complicated series of jointed cartilages or bones (cf. Figs. 24, 65). The appendages are primitively small steering and balancing organs in fishes, but they become of paramount importance in locomotion in land vertebrates. The great variations in structure in these organs will be one of the central themes in our study of vertebrate evolution.

Paired fins are poorly developed or absent in some of the lowest vertebrates. Their origin has been much debated. It seems probable, however, that they were at first merely flaps which had grown out from the sides of the body just as the median fins appear to have grown out in the mid-line of the back and tail regions; the two types of fins often have a similar structure and similar stabilizing functions and may well have had similar origins.

Branchial arch system.—A series of cartilaginous or bony bars found between the gill openings in typical vertebrates serves to stiffen the gill (or branchial) region and affords support for the muscles which open and close these slits (Figs. 6, 7). In jawless vertebrates, as far as is known, these bars form a united set of structures fused dorsally to the skeleton of the head region. In jawed forms the branchial bars are normally separate from the skull structures and are divided into upper and lower halves, bent somewhat on each other; and further subdivision usually occurs. In land types, with the loss of gill breathing, there is great reduction in this originally important skeletal system.

Jaws are absent in the most primitive vertebrates. It is believed that they have been derived from an anterior pair of gill bars, the upper (palatoquadrate) corresponding to the upper half of an arch, the lower jaw (mandible) to the main ventral segment.

As the jaws enlarge, they tend to encroach on the gill area behind them. In jawed fishes the gill openings are typically elongate slits. In some fossil fishes (placoderms) the first slit behind the jaws appears to have been of this type still (Figs. 7, 27). In most fishes, however, the jaws have pushed back so far that they crowd against the next arch (called the hyoid arch). This blocks the space occupied by the first slit, which tends to be reduced to a small hole in the upper part of the original slit area. This is termed the spiracle. As the jaw joint crowds against the hyoid arch, the main upper element of this arch—the hyomandibular—tends to assume a new function: it braces the jaw against the side of the braincase and thus aids in mastication.

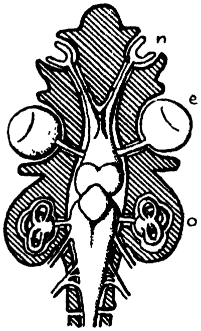


FIG. 5

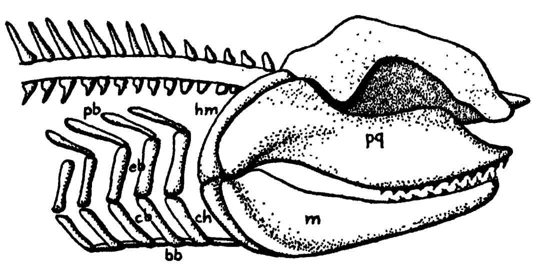


FIG. 6

FIG. 5.—Diagram to show relation of braincase to nervous system and sense organs in fishes. The braincase is represented as sectioned in a horizontal plane. The braincase forms paired capsules inclosing the nasal sacs (*n*), protects the eyeballs (*e*), and incloses the canals and sacs of the ear (*o*).

FIG. 6.—The jaws and branchial arch system of a shark, essentially the Mesozoic *Hybodus*. The braincase and spinal column are also shown. Abbreviations: *bb*, Hypobranchial and basibranchial elements of the branchial arches; *cb*, ceratobranchials, the main ventral elements; *eb*, epibranchials, the principal dorsal elements; *pb*, pharyngobranchials; *ch*, ceratohyal, and *hm*, hyomandibular, elements of the hyoid arch immediately behind the jaws; *pq*, primary upper jaw (palatoquadrate); *m*, lower jaw or mandible. (After Smith Woodward.)

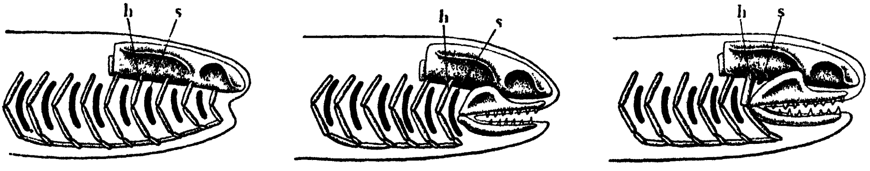


FIG. 7.—Diagrams to show stages in the evolution of jaw structures in vertebrates. *Left*, the jawless stage found in the Agnatha; the mouth was small, the gill arches similar throughout. *Center*, a stage in which jaws, evolved from one of the anterior gill bars, had developed to the stage seen in the Placodermi. One or two anterior gill slits have been eliminated, but the slit corresponding to the spiracle (*s*) of more advanced forms is still of normal type, and the hyoid arch (*h*) behind it is unspecialized. *Right*, the advanced type of jaw seen in fishes above the placoderm level. The upper part of the hyoid arch is specialized as the hyomandibular, propping the jaw joint on the braincase; the intervening gill slit is reduced to the spiracle.

Skull.—In the embryo of every vertebrate there develops a braincase, a box of cartilage inclosing the brain and articulating at its posterior end with the vertebral column (Figs. 5, 6, 55). Anteriorly, nasal capsules protect the nostrils; hollows in the sides receive the eyes; extensions from the sides of the posterior part inclose the primitive ear as otic capsules. The braincase remains cartilaginous in many fishes, but in a majority of fishes and other vertebrates it becomes more or less ossified.

In sharks the braincase and the primary upper jaws, loosely attached to it, are the only head structures. In most other fishes, however, dermal bones are present in addition. A shield of such bones covers the top and sides of the head region (Fig. 8), coming into contact with braincase and primary jaws (when present). Other dermal bones appear in the skin lining the mouth. These dermal structures tend to replace in part the deeper cranial elements and to form, with them, a unified cranial structure—the skull.

Nervous system.—The central nervous system of vertebrates consists of the brain, the spinal cord running down the body from the brain, and nerves passing out from these structures to sensory and motor end-organs. The spinal cord differs radically in position from the main nerve trunk of most invertebrates, in that it lies in a dorsal position, passing down the back above the notochord and vertebral centra and protected by the neural arches between which the nerves emerge (a pair to each segment). The brain possesses an exceedingly complicated structure, of which we may note the superficial features often revealed by casts of the inside of the braincase (Fig. 9; cf. Fig. 17). A rough division may be made into three portions—forebrain, midbrain, and hindbrain. The first has paired swellings above—the cerebral hemispheres—which, primitively associated with the sense of smell, in higher forms tend to enlarge greatly and become the seat of the highest functions of the brain. Extending up behind the hemispheres one finds a stalked pineal body, or a similar structure termed the parapineal, or both; one or the other forms a median eye in many lower vertebrates. In most vertebrates, tissues

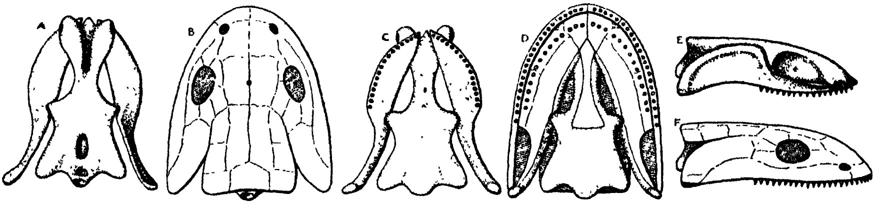


Fig. 8.—Diagrams to show comparison of the skull in forms with and without dermal bones. Cartilage or cartilage-replacement bones stippled; dermal bones white. *A*, Dorsal, *C*, ventral, and *E*, lateral views of a sharklike form, with separate braincase and "primary" jaws (cf. Fig. 55, etc.). *B*, *D*, *F*, Dorsal, ventral, and lateral views of the skull type found in bony fishes and higher forms. Dorsally and laterally the dermal bones cover the internal structures and unite them into a single mass. Ventrally a dermal element underlies the anterior end of the braincase, other dermal bones cover most of the "primary" upper jaws, and the lower margins of the roofing elements form tooth-bearing outer margins to the jaws (cf. Figs. 62, 63, 96, etc.).

from the infundibulum—a ventral projection from the forebrain—fuse with a pocket-like growth from the roof of the mouth—the hypophysis—to form the pituitary, an important gland of internal secretion. The midbrain roof has paired optic lobes, associated with sight. The main portion of the elongate hindbrain is the medulla oblongata, which has to do with touch, taste, balance, hearing, and motor responses, while above it lies the cerebellum, the "tree of life," which has control over body posture and muscular coordination.

The cranial nerves are of interest to the paleontologist, since the openings (foramina) through which they emerge are usually visible in good fossil skulls. There are always at least ten, sometimes twelve, pairs of nerves. Three go to major sense organs: I, to the nostril; II, to the eye; VIII, to the ear. Three (III, IV, VI) are small nerves which move the muscles of the eyeball. The others (V, VII, IX, X) mainly receive sensory impressions from the skin of the head and neck and lining of the mouth and convey impulses to the muscles of the jaws and throat.

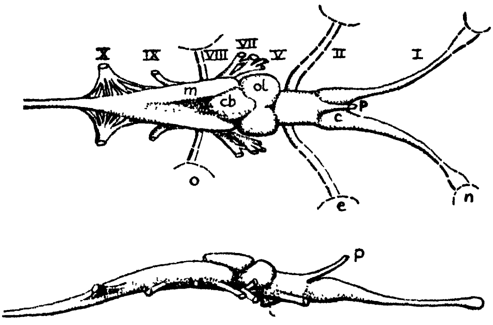


FIG. 9.—Dorsal and lateral views of restored brain and cranial nerves of *Macropetalichthys*, a Devonian placoderm. The cranial nerves are numbered (see text); the three small nerves to the eye muscles omitted. Abbreviations: *c*, cerebral hemispheres; *cb*, cerebellum; *e*, eye; *i*, infundibulum; *m*, medulla oblongata; *n*, nostril; *o*, ear; *ol*, optic lobes of midbrain; *p*, pineal organ. (After Stensiö.)

Sense organs.—All vertebrates have the three major sense organs found in ourselves—nostrils, eyes, and ears. The nostrils in primitive forms do not usually connect with the interior of the mouth but are simply a pair of pockets into which water can pass and in which the sensory cells of smell are located. In some very primitive vertebrates there is but a single nostril. In addition to the universal paired eyes, a median eye often reaches the surface (especially in older fossil forms) through an opening in the top of the skull. The primitive ear possesses no drum or earbones, as it does in higher forms, but consists merely of a series of liquid-filled sacs and canals lying entirely inside the braincase; a fish can hear only vibrations which have passed into its body and set up vibrations in its braincase. The ear seems to have been primitively a balancing organ, and that function is still important today. This sense is located in a pair of sacs and a series of semicircular canals; the canals are usually three in number, although only two (or even one) may be present in some low types.

Primitive aquatic vertebrates seem to possess a sixth sense in the lateral-line organs, situated in canals or pores extending in a line along the sides of the body and forming a complicated pattern on the head. It is believed that these organs are sensitive to water currents or pressure as an aid in swimming; and from the fact that the inner ear may communicate with the surface by a tube to the top of the head in sharks, it has been suggested that our ears (which also register movements and pressure in a liquid medium) may be but specialized portions of this same system.

Circulatory system.—We shall not be greatly concerned with the blood system in an elementary study of fossil forms, although the investigation of passages for the transmission of blood vessels is a topic of great importance in research on fossil fish skulls. We shall here note merely that, primitively, the blood is carried to the heart from the body by a series of veins; from there it is carried forward along the throat in a ventral aorta, from which branches arch up between the gill slits. After passing through capillaries on the surface of the gills, these arches reunite above, and the main current of blood passes backward to the body in the dorsal aorta. With the introduction of lungs and the reduction of gills, the system becomes, of course, highly modified.

Respiratory system.—The lower vertebrates and their relatives possess a unique breathing system of internal gills. Water passes (usually through the mouth) into the throat, thence through a series of gill chambers, where respiration occurs, to the surface of the body. In most fishes, five typical pairs of gill slits are present; originally the number may have been much higher (cf. Fig. 17). The spiracle, mentioned above, is sometimes enlarged and may function instead of the mouth as an inlet for water; in many higher fish, on the other hand, it is reduced or absent. The gill slits sometimes open separately to the surface (sharks, some ostracoderms). In most fishes, however, the gills have a common posterior opening and are covered by a structure termed the operculum. Lungs, connected with air breathing, appeared at an early stage in fish history, for they seem to have been characteristic of early bony fish and are even reported in one of the placoderms. In amphibians the gills have tended to atrophy; the spiracle becomes the eustachian tube of the middle ear; other pouches may form glands of internal secretion.

In living adult vertebrates the gill function is primarily and usually exclusively that of respiration. Very probably, however, this function was originally an incidental or secondary one. The gill system in lower chordates is mainly a feeding device; food particles are strained out from the stream of water passing through the pharynx. The gills may still have functioned in this fashion in the Paleozoic jawless fishes (ostracoderms); modern jawless types (lampreys and hagfishes) have, as adults, evolved peculiar rasping "tongues" as a substitute for jaws, but the larval lamprey is still a food-strainer.

Digestive and urinogenital systems.—We shall have little to do directly with these organ systems (jaws and teeth are discussed elsewhere), although many skeletal features are directly related to food habits and reproduction. Primitive vertebrates are, of course, egg-laying types, although even among some sharks the egg may undergo development within the mother's body. Usually the eggs are unprotected in water-living forms, although in some cases (skates and chimaeras, for example) a hard egg case, capable of preservation, is present.

Muscular system.—Although muscles are practically never preserved, these organs are of importance to us since they are so intimately associated with the skeleton. Somewhat comparably with the skeleton, the muscle system may be divided into axial, branchial arch, and appendicular series. The axial muscles constitute the main means of locomotion and the greater part of the bulk of water-living vertebrates. They are arranged segmentally in a series of layers down the back and flanks of the fish. Between each successive segment lies a rib; opposite each segment lies a vertebra. It is probable that the segmentation of the skeleton took place primarily in relation to that of the muscles. The small muscles which move the eyeball are probably highly modified portions of this axial group. A special group of muscles is that associated with the branchial arches; the muscles of the jaws, when these structures are formed, were derived from this group. With the development of limbs, strong sets of muscles form above and below the skeletons of these appendages.

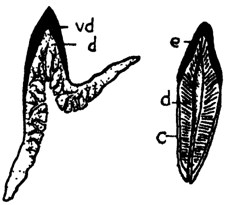


FIG. 10.—Denticle of shark (*left*) and mammalian incisor (*right*). Abbreviations: *c*, cement; *d*, dentine; *e*, enamel; *vd*, vitrodentine (analogous to enamel).

Skin derivatives.—Not only membrane bones, previously discussed, but other structures may arise in the outer layers of the body. From the most superficial portion of the skin are formed, in various groups of higher vertebrates, horny scales, claws, true horns, feathers, or hair; these are usually incapable of fossilization. From deeper layers in the skin of many fishes are formed denticles, typically hollow cone-shaped structures, mainly composed of compact dentine and covered with a film of very hard, shiny, enamel-like material (Fig. 10). In typical sharks such denticles are scattered over the surface of the skin, giving it a rough, sandpaper-like texture; while in many early and primitive fishes they form a surface covering for underlying dermal bones or scales. Teeth are very similar in composition to denticles and are thought to have had a similar origin.

Primitive chordates.—The vertebrates, although a large and important group of animals, do not in themselves constitute a major division of the animal kingdom but are grouped together with a small number of other living forms of more primitive character to form the phylum Chordata, animals with a notochord. These other types are almost entirely unknown as fossils but must be considered briefly because of their bearing on the origin and early history of the vertebrates.

Amphioxus.—The Cephalochorda comprise but a few small marine forms, such as *Amphioxus* (Fig. 11). This animal has the appearance of a small translucent fish; but structurally it is far inferior to any of the true vertebrates. There are no bones or cartilages, no paired fins or limbs, no jaws or teeth; there is little indication of a brain and only vestiges of sense organs. There are, however, a number of features which tend to show that *Amphioxus* is related to the vertebrates. Although hard skeletal parts are absent, there is a well-developed notochord; a dorsally situated nerve cord runs the length of the body; and breathing is accomplished by means of numerous internal gills.

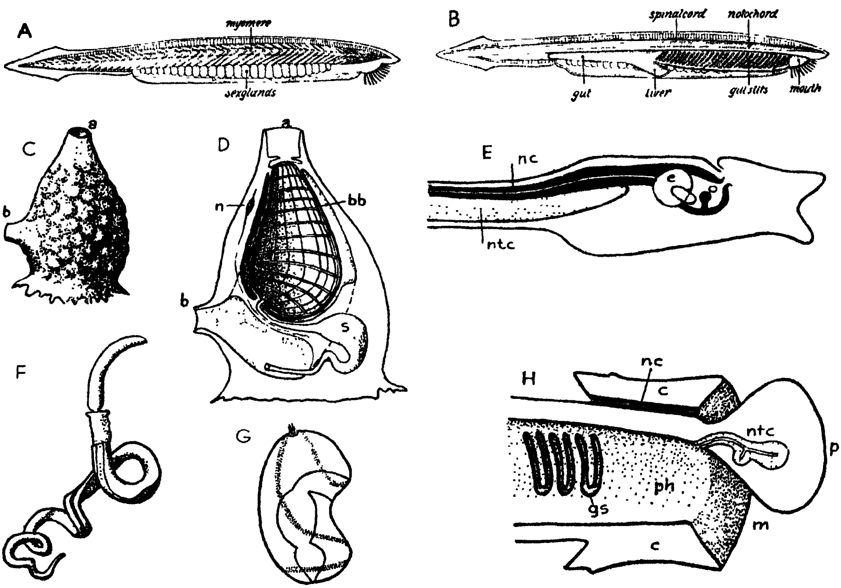


FIG. 11.—Lower chordates. *A*, *Amphioxus*, superficial view; *B*, median section. *C*, External view of a simple tunicate; *a*, incurrent opening; *b*, excurrent opening. *D*, Section of simple tunicate; *bb*, branchial basket; *n*, nervous system; *s*, stomach. *E*, Section of trunk and part of tail of larval tunicate (simplified); *e*, rudiment of eye; *nc*, nerve cord; *ntc*, notochord; *o*, otocyst (rudimentary ear). *F*, Adult acorn worm. *G*, Larval acorn worm; the stippled areas are ciliated bands comparable to those of echinoderm larvae. *H*, Diagrammatic sagittal section through anterior part of body of acorn worm; *c*, collar; *gs*, gill slits; *m*, mouth; *nc*, nerve cord; *ntc*, notochord; *p*, proboscis; *ph*, pharynx. (*A*, *B* from Gregory, after Delage and Hérouard; *C–H* mainly after Delage and Hérouard.)

Such characters strongly suggest that this form lies near the stem of the vertebrates; and it is of interest that the larva of the lamprey, most primitive of living vertebrates, is similar to *Amphioxus* in many structural details. *Amphioxus,* itself, however, is generally believed to be debarred from any ancestral position because of such specializations as the forward extension of the notochord to the tip of the head (hence the name of the group) and the development of a pouch covering the gills—features seemingly connected with burrowing habits. It is possible that *Amphioxus* is a degenerate, rather than a truly primitive, form.

Tunicates.—The Urochorda include a considerable number of marine animals known as the tunicates or sea squirts; the central types are perhaps the solitary, sessile forms found as adults attached to rocky surfaces in shallow waters. They are motionless, shapeless masses covered with a leathery tunic. Water is drawn in through an opening at the top and passed out through a second orifice at the side of the body. Superficially, they are quite unlike vertebrates or even *Amphioxus,* and internally the resemblances are, at first sight, not much greater. There is no notochord, no nerve cord. The water drawn in is strained through a barrel-like structure which occupies the greater part of the interior of the creature. Food particles collected here pass through an opening at the bottom of the barrel to the stomach and intestine, and the feces pass out through an anus into the current of water leaving the body through the lateral opening.

But this barrel which strains the food is also the breathing organ of the animal and consists of a much-elaborated set of internal gills. Confirmation of this suggestion of chordate nature is furnished by the study of the embryo, which, unlike the adult, is a free-swimming, tadpole-shaped animal with a long tail in which are found both a dorsal nerve cord and a well-developed notochord. Later in life the tunicate becomes attached to a rock, and the tail (and with it the notochord and most of the nerve cord) disappears. It seems probable that the tunicates are degenerate descendants of forms related to *Amphioxus.*

The acorn worms.—Most characteristic of the Hemichorda are the acorn worms, so called because at the anterior end of the elongate body is a tough, proboscis-like digging organ with a collar behind it, the two together somewhat resembling an acorn in its cup. The body, although wormlike in appearance, is in structure radically different from that of the common worms; and its true chordate nature is shown by the presence of numerous gills slits similar in structure to those of *Amphioxus.* Much of the nervous system is rather diffuse, but there is a dorsal nerve cord in the collar region; and a rudimentary structure in the head may be homologous with the notochord. Altogether, it would seem that the acorn worms and their relatives are a specialized offshoot from the base of the chordate stock.

The tiny larva of the acorn worm is very similar in appearance and structure to the larvae of certain echinoderms, and for a long time was thought to belong to that group.

These living lower chordates are obviously types which are related to the vertebrates but which differ in being more primitive, specialized, or degenerate. Fossil lower chordates are unknown, since there are no hard parts capable of preservation.

Vertebrate ancestry.—At one time or another the ancestry of the vertebrates has been sought in almost every invertebrate group (Fig. 12). Some have suggested that vertebrates have been derived directly from the coelenterates, the simplest of the metazoans. Obviously, these forms may have been the original ancestors; but they lack so many structures which are found both in vertebrates and in many other invertebrates that it seems much more reasonable to believe that the splitting-off of the group lay somewhat higher in the scale.

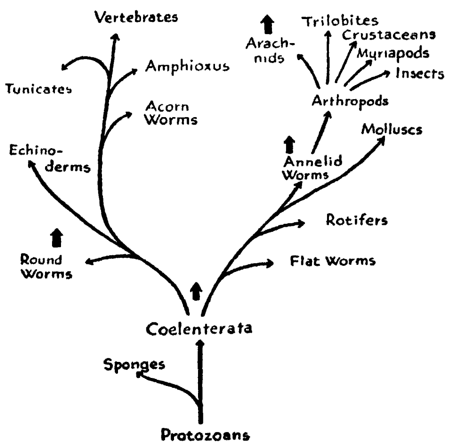


FIG. 12.—Simplified family tree of invertebrates and lower chordates; the heavy arrows indicate groups which have been advocated as ancestors of the vertebrates by various authors.

A theory of descent of the vertebrates from the annelid worms has been advocated. These animals are bilaterally symmetrical, as are vertebrates; they are segmented (as are vertebrates in backbone, nerves, and muscles); and they have a well-developed nerve cord. The nerve cord lies on the ventral side of the worm; but if the form be supposed to have turned over, the nerve cord would be on the dorsal side. But such diagnostic vertebrate structures as gill slits and notochord are not found in annelid worms; and since the mouth of the annelid was on the under side of the head, we should expect that the mouth of vertebrates would lie on the back of the head unless we suppose that the old mouth has closed and a new one formed.

The arthropods, most highly organized of invertebrates, have also been strongly advocated as vertebrate ancestors, especially the arachnids, a group including not only the spiders but the scorpions and a number of such water-living types as the horseshoe crab and the extinct water scorpions —the eurypterids. Arachnids have an external, not an internal, skeleton; but some of the earliest fossil vertebrates had a highly developed armor which in some cases greatly resembled that of aquatic arachnids. It has been suggested that this resemblance denotes a real relationship. According to this theory, however, it should be the under surface of one group which should resemble the dorsal side of the other (for the nerve cord, as in annelids, lies ventrally in arachnids). Unfortunately, this is not the case; and, just as in the case of the worms, there are great difficulties involved in assuming a reversal of the top and bottom sides of the animal. In addition, it is necessary to do away with the jointed limbs and other complicated structures of the arthropod and remake the entire animal. There is no positive evidence of such a radical rebuilding. Further, the theory implies that the lower chordates are unrelated to the vertebrates, despite the many similarities in structure.

The most reasonable theory of vertebrate origin seems to be that which uses the evidence derived from the primitive chordates. While *Amphioxus*, tunicates, and acorn worms are obviously not in themselves actual vertebrate ancestors, it is highly probable that they are specialized or degenerate relatives of these ancestors. And we have noted a suggestive point—that the larva of the acorn worms, simplest of chordates, is similar to that of the echinoderms.

No group, at first sight, would seem to be farther removed from the vertebrates than the starfish and sea urchins, with their radial symmetry and various peculiar and complicated organs. No one would derive the vertebrates from echinoderms as we now know them. But it is not impossible that both may have been derived from a form similar to the echinoderm and acorn-worm larva, a form advanced above the coelenterate level of organization but still a rather generalized, bilaterally symmetrical animal. From it, with the development of sessile life and of radial symmetry, might have arisen the first echinoderms; on the other hand, forms tending to become increasingly actively swimming types would presumably have retained bilateral symmetry and developed locomotor organs in the way of muscles, notochord, and, finally, the vertebrate skeleton.

Under this theory the early ancestors of the vertebrates would have been small, soft-bodied animals, practically incapable of preservation as fossils. Hence it is almost hopeless to expect paleontology ever to give us any record of the earliest vertebrate ancestors.

Classification of vertebrates (Fig. 13).—Most of the classes into which vertebrates should be divided are obvious. The higher types include the mammals (class Mammalia), birds (class Aves), reptiles (class Reptilia), and amphibians (class Amphibia). The lower, water-living types are often regarded as forming a single class—the fish, or Pisces. But some subdivision of this last group seems necessary. Superficially, the various kinds of "fish" seem quite similar in nature; they are all water-living types and in that connection have many features in common. But in structure there is a vast amount of variation. A lamprey and a codfish, for example, are in many respects as different as a frog and a man; and it is not reasonable to "lump" them in a single class. The lampreys and hagfishes, together with related fossils forms, may be grouped as the class Agnatha, primitive vertebrates without typical limbs or jaws. Certain primitive fossil fishes in which jaws and paired appendages are present but peculiarly constructed may be considered as constituting a class Placodermi. The sharks and their relatives comprise the class Chondrichthyes; the higher bony fish, the class Osteichthyes. Although it is hardly necessary to group the various classes formally into superclasses, we may for convenience use the term Pisces ("fish") to include all the primitive water-living groups, in contrast to the Tetrapoda ("four-footed"), the land-dwelling classes. Another method of grouping is to contrast the Amniota (reptiles, birds, mammals; cf. p. 163) with Anamnia; we may in many respects conceive of the Amphibia as merely a sort of progressive fish.

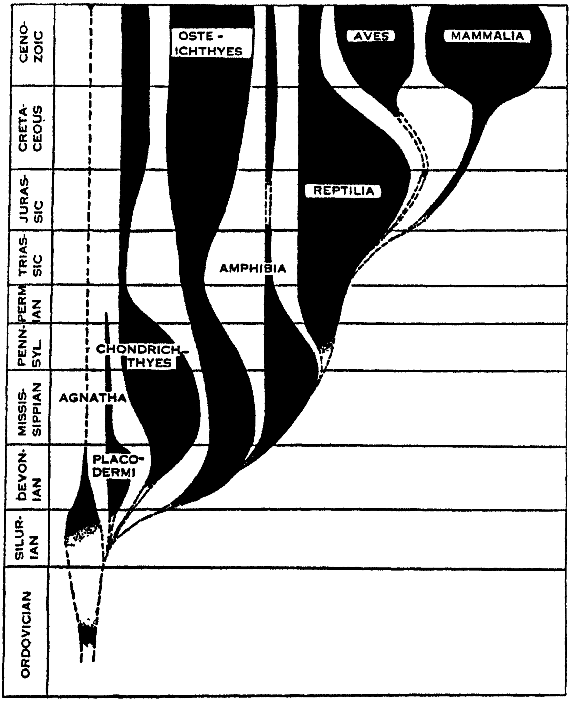


FIG. 13.—A family tree of the vertebrate classes. A rough indication of the comparative abundance of the various groups is furnished by the thickness of the various branches.

Pisces	Class Agnatha	Anamnia
	Class Placodermi	
	Class Chondrichthyes	
	Class Osteichthyes	
Tetrapoda	Class Amphibia	
	Class Reptilia	Amniota
	Class Aves	
	Class Mammalia	

CHAPTER 2

PRIMITIVE JAWLESS VERTEBRATES

THE lampreys and hagfishes, usually termed the "cyclostomes," are outstanding among living vertebrates in the presence of seemingly primitive characters. These peculiar forms of eel-like appearance are quite devoid of jaws such as characterize all other living vertebrates and are limbless, whereas all other living groups of fishes have well-developed paired fins. Turning to fossil types, we find that the most ancient of known vertebrates were forms usually grouped as the ostracoderms. These fishes were almost always incased in a heavy armor of bone or other hard material and thus seem quite unlike the soft-skinned modern cyclostomes in which the skeleton is entirely cartilaginous. But there, too, jaws appear to have been totally absent and limbs, at the most, poorly developed. It is probable that the living cyclostomes and the fossil ostracoderms are members of a common stock of primitive ancestral vertebrates which we may term the class Agnatha, jawless vertebrates.

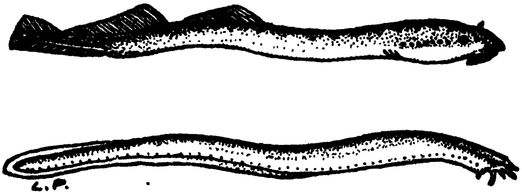


FIG. 14.—Living cyclostomes. *Above*, the lamprey *Petromyzon; below*, the hagfish *Myxine*. (After Dean.)

Cyclostomes.—The living agnathous forms include the lampreys, such as *Petromyzon*, and the hagfishes (*Myxine, Bdellostoma*) (Fig. 14). They are semiparasitic in habit, attaching themselves to fish and living on their flesh. The body is elongate, eel-shaped; there are no scales or denticles in the tough and slimy skin. Paired fins are absent, although median fins are developed. From six to fourteen pairs of gills are present; these differ from the slitlike structures of other living vertebrates in being spherical pockets connected with the inside and the surface by small tubes. In the lampreys the margins of the round, jawless mouth form a sucking disk for attachment to the prey; in the hagfishes the mouth is surrounded by tentacles. Jaws are functionally replaced by a long protrusile "tongue," armed with a patch of horny structures resembling teeth; this forms an efficient organ for rasping away the flesh of the lamprey's prey. There are paired eyes and a median pineal eye (well developed in lampreys, vestigial in hagfishes). Instead of the three semicircular ear canals of most vertebrates, lampreys have but two and hagfishes one. The olfactory organs are still more peculiar, for, instead of the double nostril found in all other living vertebrates, there is but a single median nasal sac.

The skeleton consists of uncalcified cartilage. The braincase is a rather specialized and complicated structure. An elaborate system of branchial arches is present in the lamprey; but these arches, instead of being separate elements, are fused into a peculiar basket inclosing the gills, while part of the branchial skeleton is modified into a support for the "tongue." The notochord is large and unrestricted. All forms have cartilaginous supports for the median fins, while *Petromyzon*, although lacking vertebral centra, has a row of small neural arches.

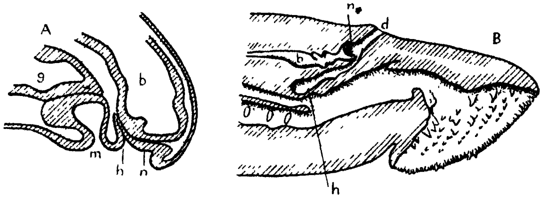


FIG. 15.—Diagrams to show the development of the dorsal nostril of lampreys. *A*, Longitudinal section through the head of a larval lamprey, showing the central position of the nostril and hypophysis; *B*, a later stage, in whych hypophysis and nostril have migrated dorsally. Abbreviations: *b*, brain; *d*, dorsal common opening of hypophysis (*h*) and nostril (*n*); *g*, gut; *m*, mouth. (After Goodrich, simplified.)

A striking difference between the lampreys and the hagfishes is shown in the position of the single nostril. In most vertebrates the nasal openings are near the front of the head, or even slightly on the under side. In the hagfishes the nostril opens at the tip of the "snout," but in the lampreys a large "upper lip" grows out from the front of the roof of the mouth to form the tip of the body; the originally ventral nostril (together with a second pocket-shaped structure, the hypophysis) is forced around forward and upward until in the adult it is found opening downward high on the top of the head just in front of the eyes—a situation unparalleled in other living vertebrates (Fig. 15).

Possessing no bones, true teeth, or other hard parts capable of preservation, the cyclostomes are unknown as fossils. Certain small Paleozoic tooth-like structures—conodonts—have been thought to be cyclostome "teeth"; but conodonts are apparently of invertebrate origin.

The lampreys and hagfishes are obviously lower in their plane of organization than any other living vertebrates. But, before concluding that they are really primitive types, we must take into account the fact that these forms are semiparasitic and that parasites are generally specialized and degenerate rather than truly primitive forms. Specialized they undoubtedly are in such respects as the peculiar "tongue." May it not be that many of the features of simplicity in their structure are really due to losses associated with parasitism rather than to true primitiveness? We may seek an answer in the study of related fossil types. As will be seen, many cyclostome features were present in the oldest-known fishes.

Ostracoderms.—The oldest certain remains of vertebrates are fragments contained in Ordovician rocks from Colorado and other western states. The nature of the sediments suggests that these remains are the debris of forms living in inland waters, which, after death, were washed out into a shallow bay. This supports the theory that the vertebrates were of fresh-water origin and helps to explain the almost utter absence of vertebrate remains in the dominantly marine sediments of the early Paleozoic. The fragments are too small to allow us to gain any idea of the appearance of these early types, but their microscopic structure shows that we have to do mainly with pieces of armor such as are found covering the bodies of vertebrates in the subsequent periods. It is of particular interest that some of these specimens show that bone had already developed in the earliest stage of known vertebrate history.

It is not until late Silurian and early Devonian times that we gain any adequate idea of these forms or, rather, their successors. Then, as the Silurian draws to an end, we find increasingly numerous remains of vertebrates quite unlike any existing forms in appearance. Almost all are covered with varied types of armor, a feature to which the name "ostracoderms" ("shell-skinned") is due. In some forms the internal skeleton of the head region is highly ossified; in others it is persistently cartilaginous; and in none have remains of the axial skeleton as yet been found. In bodily outlines and in the presence of hard skeletal parts they seem remote from the cyclostomes; but we find that all these forms, like living lampreys and hagfishes, are characterized by the absence of jaws and by the absence or poor development of paired fins; and that, further, those which are best known show striking resemblances to the cyclostomes in many structural features. When we first see them, these ostracoderms have already had a long history behind them and are divided into several distinct groups.

Osteostraci.—*Cephalaspis* and its relatives constituting the order Osteostraci are known in more detail than any other ostracoderms, and hence merit first consideration. These types are abundant in late Silurian and Lower Devonian rocks, while a few forms lingered until the close of Devonian times.

Few were of great size, the length ranging generally from a few inches to a foot or two. They were completely incased in an armor of plates and scales. When sectioned, these plates are seen to be composed of true bone, while on the surface was a tuberculated layer of dentine comparable to fused dermal denticles. The body scales were arranged in a series of vertical rows, each containing but a few elongate members. The body (Fig. 16) was rather fishlike in appearance, with one or two dorsal fins and a heterocercal caudal. The head was much flattened, the body higher, with a flat ventral surface and a triangular section. Structures are present which appear to be paired fins of a sort. At either lateral margin a continuous series of scales projects outward to form a fin fold somewhat comparable to a pelvic fin. Behind the head shield there are, in most genera, scale-covered flaps which are comparable to pectoral fins; their internal structure is unknown. The head (Figs. 17, 18)—in fact, the whole area back to the shoulder region—was covered dorsally by a nearly solid shield of bone; in all but a few of the older and presumably more primitive genera there were prominent "horns" at the posterolateral corners. The eyes, directed upward as in many bottom-living types, were situated close together near the center of the shield; between them lay a median plate with an opening for the pineal eye. Anterior to this plate was a slit comparable to that which in lampreys contains the opening for the single nostril and hypophysis. In the center of the skull, behind the eyes, was an area filled by a series of small polygonal plates, and there were similar areas near each margin.

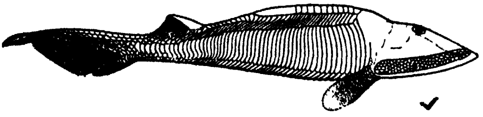


FIG. 16.—*Hemicyclaspis*, a characteristic cephalaspid of the late Silurian and early Devonian. About ⅓ natural size. (After Stensiö.)

The shield folded under onto the margins of the flattened ventral surface. Behind its front edge was a small and obviously jawless mouth, while posterior to this a series of movable plates covered the throat region. At the edge of these plates were round external openings for the numerous gill pouches.

Recent work has disclosed much of the internal structure. It was long supposed that, while ostracoderms had superficial armor plates, the internal skeleton was purely cartilaginous. But in *Cephalaspis* an ossified cranial skeleton was present. Its composition was in contrast to that of most vertebrates; for, instead of a separate braincase and jointed branchial arches, there was a single unified structure underlying the entire dermal shield. This seems, at first sight, a highly specialized feature; but it is possible that it is really a primitive undifferentiated condition and that the establishment of independent units was a later development.

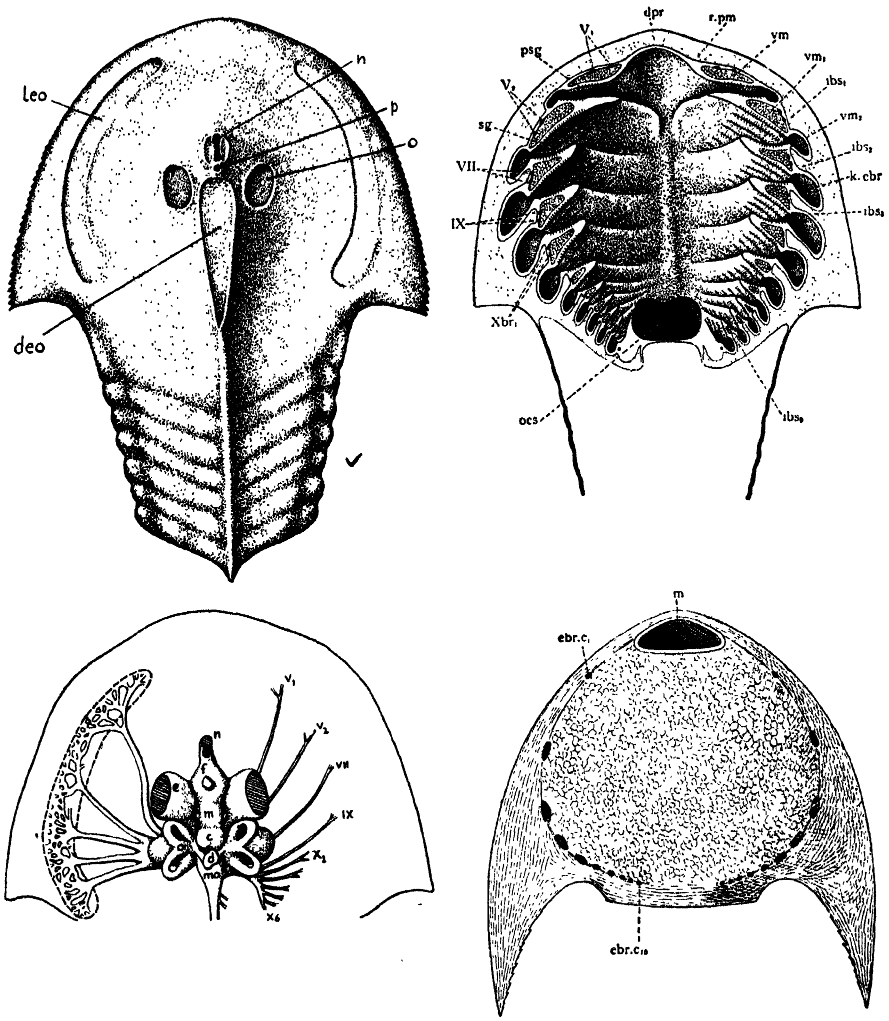


FIG. 17.—The cranial anatomy of *Kiaeraspis*, a cephalaspid. *Upper left,* top view of head and anterior part of trunk region: *deo,* supposed dorsal electric organ, *leo,* supposed lateral electric organ; *n,* opening of single dorsal nostril and hypophysis; *o,* orbit; *p,* pineal opening. *Lower left,* diagrammatic dissection of top of head, to show brain, nerves, and sense organs. Nerves to supposed electric organ shown on the left; other major nerves (numbered) on right, arranged in a series corresponding to the gill slits. *c,* Cerebellum; *d,* nerve to dorsal electric field; *e,* orbit; *f,* forebrain; *m,* midbrain; *mo,* medulla oblongata; *n,* opening for nostril and hypophysis; *o,* ear region (two canals). In this and the next figure Roman numerals indicate cranial nerves. *Upper right,* restoration of ventral surface of head, with the plates covering the throat removed, showing the ten gill sacs and the small, anteriorly placed mouth. *dpr,* Mouth; *ibs,* partitions between gill sacs; *kcbr,* ducts from gill pouches to surface; *oes,* oesophagus; *psg,* a prespiracular gill pouch lost in higher vertebrates; *rpm,* rostral region in front of gills; *sg,* gill pouch corresponding to the spiracle of higher fishes; *vm,* muscles of gill pouches. *Lower right,* restoration of ventral surface of head, covered by small plates; *ebrc,* opening of the gills; *m,* mouth. (After Stensiö.)

From the internal cavities most of the structure of the soft parts of the head can be made out. The brain and nerves and blood vessels are found to have been quite similar to those of lampreys and seem to show a very primitive vertebrate pattern. In the ear there were two semicircular canals, as in the lampreys; the dorsal slit referred to above is seen to lead into cavities which obviously lodged a single nostril and hypophysis in lamprey-like fashion. Ten pairs of gill cavities were present; their morphological relations show that it is the third of these gill pouches which corresponds to the spiracle with which the gill series of jawed vertebrates commences; two pouches are present here which have been crowded out of existence in higher vertebrate groups.

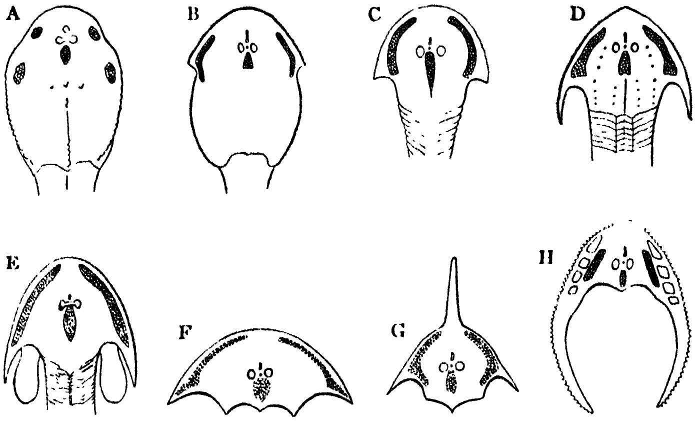


Fig. 18.—Dorsal view of the head shield in various osteostracans. *A–E*, A morphological series showing reduction in the amount of trunk region included in the cephalic shields and in the development of pectoral fins and "horns." The fins (seldom preserved) are known in this series only in *Cephalaspis*. In *A* a large proportion of the trunk is included in the shield, and pectoral fins were not developed; in *E* most of the trunk has been freed from the head shield, large sinuses for the attachment of pectoral fins are present; *B–D* show intermediate conditions: *A*, *Tremataspis; B*, *Didymaspis; C*, *Kiaeraspis; D*, *Thyestes E*, *Cephalaspis; F*, *Benneviaspis; G*, *Boreaspis; H*, *Sclerodus*. (Mainly after Stensiö.)

Beside the ordinary nerves of the head, very stout nerve trunks (Fig. 17) are found running to the polygonal plate areas, mentioned previously. These may be sensory in nature, but they are exceptionally large, and it has been suggested that these areas lodged powerful electric protective organs, such as are present in certain skates, eels, and catfish today. It is surprising to find such highly specialized structures in such an early form; but we must remember that by late Silurian times the vertebrates must already have had a long, even if unknown, evolutionary history behind them, and these small forms had large predaceous invertebrates as contemporaries.

The Osteostraci were a homogeneous group as regards their fundamental structures. There is, however, considerable variation in the contours of the head (Fig. 18): there are great differences in the degree of development of the "horns"; the head may be broad or slender; a long rostral spine may be developed; the plate-areas may vary in size, and the lateral ones may be subdivided. *Tremataspis* is a Silurian genus which may be relatively primitive in nature. Here there are no "horns" or pectoral fins; instead, the head tapers smoothly back into the trunk, and a considerable portion of the trunk armor is fused with the head shield. Such an animal would have swum rather inefficiently, and with little steering ability, by a tadpole-like, wriggling of the posterior part of the body. In *Cephalaspis* and other later genera a freeing of body segments from the shield would give greater mobility to the body, and the development of pectoral fin flaps would aid greatly in balance and control of direction. A similar development of paired-fin structures will be seen in other early vertebrates.

The cephalaspids were obviously, from their depressed shape and dorsally situated eyes, bottom-dwelling forms; their small mouths and expanded gill chambers suggest that they were forms which made their living by straining food particles from the mud of the stream bottoms.

It is obvious that these ancient types were fundamentally quite close to the modern lampreys in structure. Can the lampreys have descended from them? Many of the differences may be correlated with a change from a bottom-dwelling to a semiparasitic mode of existence. The most striking contrast lies between the well-ossified skeletal system of the ancient types and the purely cartilaginous skeleton of the lampreys. But similar degeneration is known to have occurred in other groups; and, despite their superficial dissimilarity, the osteostracans may possibly have been ancestral to the lampreys.

Anaspida.—The order Anaspida includes a number of genera, such as *Birkenia* (Fig. 19) and *Lasanius*, which were widespread in the late Silurian; there were late survivors in the Upper Devonian of Canada. None was more than 10 inches in length, most about half that size. In the typical Silurian genera there was a complete covering of dermal armor, composed of a noncellular bony material. This appears to be the equivalent of the basal layer of the scales and plates of other early vertebrates and is suggestive of a stage in armor reduction. Scales arranged in regular rows covered the body; and the head region was protected by a complicated pattern of small plates, which appear to be more or less fused into a shield on the dorsal surface. Unlike any normal vertebrate of later times, the tail tilted downward, rather than upward, to give a "reversed heterocercal" type of caudal fin, found among living animals only in the larval lamprey. So unexpected was this find that for many years these forms were restored bottom side up.

A series of spines lay along the dorsal side of the body. An anal fin was present. Of paired fins there were none in the typical Silurian genera, but there was a prominent, projecting spine in the position of a pectoral fin, and other spines more posteriorly placed. Behind the head a row of small, circular openings slanting back and down formed the exits from a series of gill pouches.

No trace of internal structure has been discovered; the skeleton was presumably cartilaginous. The dermal armor, however, reveals that the head structure (Fig. 19) was fundamentally similar to that of *Cephalaspis*. The two large orbits were somewhat farther apart and faced more laterally than in that form. Between them lay a plate pierced by an opening for the pineal eye; while the nostril, just as in the last order and in the lampreys, reached the surface through an opening high on the top of the head. The mouth was shaped more like that of higher vertebrates than in other agnathous types, but it is improbable that true jaw structures were connected with it.

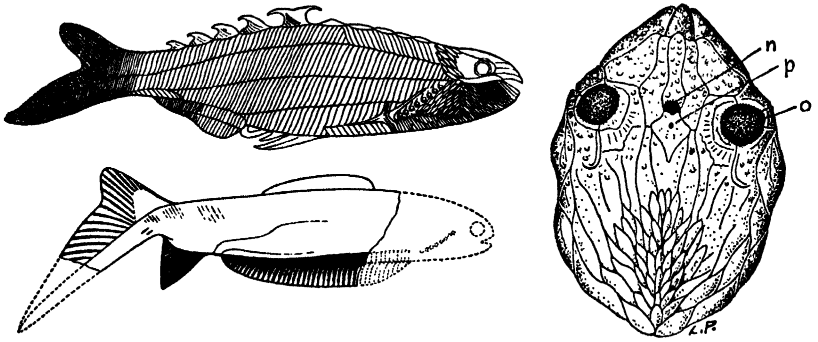


FIG. 19.—Anaspids. *Upper left, Birkenia* from the late Silurian of Scotland; original about 4 inches long. (From Stetson.) *Lower left, Endeiolepis,* from the Upper Devonian of Canada; length about 8 inches. (From Stensiö.) *Right,* dorsal view of the head plates of *Pharyngolepis,* a late Silurian anaspid from Norway, showing the lateral (*o*) and pineal (*p*) eyes and the single nostril (*n*). (After Kiaer.)

Considerable variation from this typical structure is found in other anaspids. *Lasanius* of the Upper Silurian had lost most of its armor, except for the dorsal spines and a series of pectoral spines and their supports. Still more divergent is *Endeiolepis* of the Upper Devonian (Fig. 19). The body was almost completely naked, and the dorsal spines were replaced by a long, soft dorsal fin. Ventrally, a continuous fin fold, stiffened by scales, ran the length of the trunk on either side and formed a structure comparable to both pectoral and pelvic fins of higher vertebrates. It may be that this unique structure is primitive for anaspids and that the paired spines found in other genera are remnants left after its degeneration; on the other hand, this fin development may have taken place within the anaspids parallel to fin evolution in other vertebrate groups.

That these forms were related to the Osteostraci is obvious; they were, however, less depressed and seemingly more active types, suggesting a trend away from the comparatively sedentary, bottom-living existence which may have characterized the earliest jawless vertebrates. They may well have been even more closely related to the lampreys than *Cephalaspis*. It seems probable that the anaspids were undergoing reduction of armor; with the loss of the remainder of the dermal skeleton, the anaspids would be suitable lamprey ancestors.

Heterostraci.—A very different group of jawless vertebrates is the order Heterostraci, whose members (like the cephalaspids) were abundant in the late Silurian and early Devonian but had disappeared completely by the end of the latter period. Perhaps the Heterostraci may be considered the oldest of all vertebrate orders, for some of the fragmentary dermal plates from the Ordovician appear to show a microscopic structure of heterostracan type. *Pteraspis* (Figs. 20–22) is the best-known member of the group; *Poraspis* (Fig. 22), *Palaeaspis*, *Anglaspis* (Fig. 22), and *Cyathaspis* are other characteristic forms. Usually there was a complete armor comparable to that of *Cephalaspis*, but lacking bone cells. In contrast with the cephalaspids and

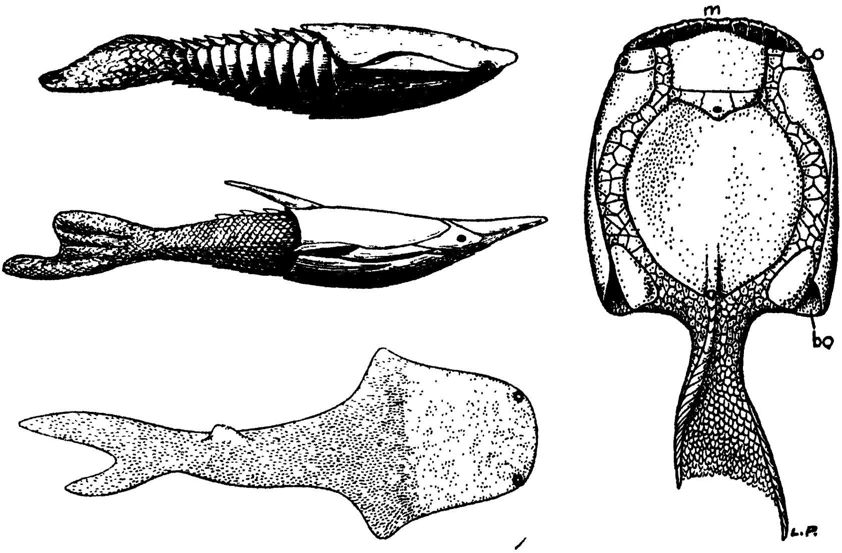


FIG. 20.—Heterostraci and coelolepids. *Upper left*, *Anglaspis* from the Upper Silurian of Spitzbergen; length about 6 inches. (From Heintz after Kiaer.) *Left center*, *Pteraspis* from the Lower Devonian of England; length about 2¼ inches. (From Heintz after White.) *Lower left*, the coelolepid *Thelodus* of the late Silurian, length of original specimen about 3–8 inches. (From Traquair.) *Right*, dorsal view of *Drepanaspis*, a flat-bodied Lower Devonian heterostracan; the general plate arrangement is comparable to that of pteraspids; original about 1 foot long. *bo*, Branchial opening; *m*, dorsally situated mouth; *o*, orbit. (After Traquair, Kiaer, and Heintz.)

anaspids, the paired eyes were far apart on the sides of the head, the pineal eye often failed to pierce the top of the skull, and a striking difference lies in the fact that there was no opening for a dorsal nostril. The body was covered by scales, often diamond-shaped. In typical heterostracans the body was little flattened. The tail fin was of the reversed heterocercal type. There are no other median fins or paired fins, but there are dorsal and ventral spines on the trunk; frequently a prominent dorsal spine arises from the back of the head shield.

The anterior part of the body, including the large gill chamber, was protected by stout armor (Fig. 21). In the more primitive Silurian types this consisted of a single oval dorsal shield, a similar ventral element, and a pair of lateral gill plates. In later types there is a tendency for the armor to break up into a number of smaller elements. In *Pteraspis*, for example, there separates from the dorsal shield an anterior rostral element and smaller plates about the orbits.

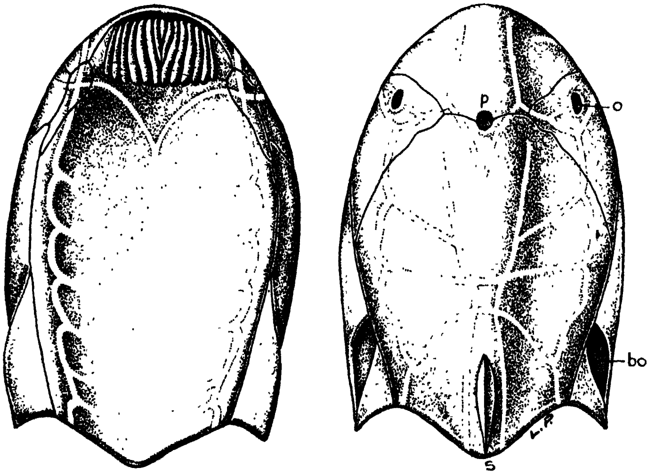


FIG. 21.—Ventral and dorsal views of the anterior portion of the body of *Pteraspis*. Lateral-line canals are indicated. The mouth lay in front of the slender series of plates near the anterior end of the ventral surface. Abbreviations: *bo*, common opening of the gill pouches; *o*, orbit; *p*, pineal opening; *s*, median dorsal spine. About twice the size of the original. (After Kiaer.)

A single lateral opening was a common outlet for the gills; the position of the gill pouches is shown by a series of five to nine paired impressions on the inner surface of the dorsal shield.

On the under side of the rostrum a transverse slit indicates the position of the mouth. In some specimens, depressions in the inner surface of the rostral shield above the corners of this slit demonstrate that the nasal sacs were situated here and were paired structures, as in higher vertebrates.

There were no jaws, but the mouth slit is bounded posteriorly by a series of parallel movable plates, suggesting that some type of nibbling movement was possible. No internal skeletal structures have been discovered; presumably, they were cartilaginous.

Considerable diversity is encountered among the known heterostracans. We have no knowledge of the appearance or structure of supposed Ordovician Heterostraci. The Upper Silurian genera, such as *Poraspis* and *Cyathaspis*, are more heavily armored than the Devonian forms and with the armor concentrated in a smaller number of plates. There is great variety, too, in the shape of the "head" (Fig. 22); in some the rostrum is short and rounded, in others greatly elongated.

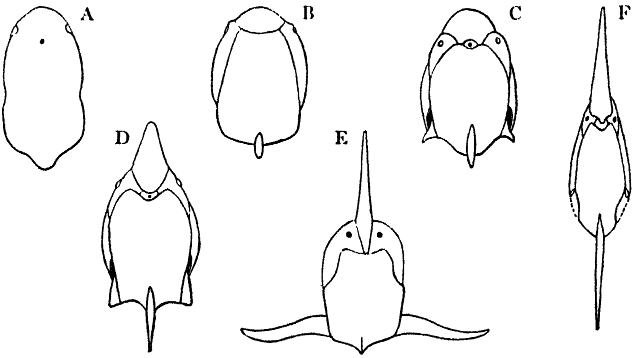


FIG. 22.—The armor in a varied series of Heterostraci: *A*, *Poraspis*; *B*, *Cyathaspis*; *C*, *Pteraspis*; *D*, *Pteraspis rostratus*; *E*, *Dyreaspis*; *F*, *Pteraspis dunensis*. *A–C* show a series in the breakdown of the originally solidly co-ossified shield into separate elements, and the development of a dorsal spine and lateral projections behind the gill opening; *D–F* show variations in the development of these structures and of the rostrum. (After Heintz, White, and Gross.)

Flattened, bottom-dwelling relatives of the pteraspids are represented by *Drepanaspis* (Fig. 20) and other Devonian genera. The head and gill region, corresponding to the area included in the pteraspid shield, is very broad and flat but is covered by a series of larger and smaller plates generally comparable with those of *Pteraspis*. The eyes were quite small; the mouth apparently was similar to that of *Pteraspis*, but in the fossils it appears at the front end of the upper rather than the under surface.

The Heterostraci are obviously not closely related to the agnathous forms previously considered—cyclostomes, Osteostraci, Anaspida—all of which are peculiar in the possession of a single dorsal nostril. Possibly the Heterostraci are the remnants of a generalized primitive vertebrate group which might have given rise, by modification and specialization, to other jawless types. Still further, it is possible that the Heterostraci may be close to the line of ascent to jawed types, in which paired nostrils were retained. Known forms of the order, however, appear to be too late in time or too specialized on their own account to be considered as such ancestors.

Coelolepids.—In the late Silurian and Lower Devonian are found a number of poorly known and tiny fishes which may be grouped in the order Coelolepida. *Coelolepis*, *Thelodus* (Fig. 20), and *Lanarkia* are representative genera. In many instances these forms are known only from patches of the scales which covered their bodies. These were minute structures, not overlapping but nevertheless forming a continuous covering for the body and hence to be considered as true scales rather than as dermal denticles of the shark type. In a few cases the complete body outline is known, but, even so, our knowledge of these fishes is slight. We know almost nothing of internal structures and very little even of superficial features. The tail is forked and apparently of the reversed heterocercal type; an anal fin may be present. The anterior part of the body (including the gill chamber) is broad and presumably flattened, as in most other ostracoderms. Flaps at the posterior end of this region in *Thelodus* may mark merely the region of the gill opening, as in Heterostraci, or may possibly be rudimentary pectoral fins, as in cephalaspids; in *Coelolepis*, however, these flaps are absent, and the head region tapers evenly into the trunk contours. In some instances pigment spots or openings show that the paired eyes were laterally placed; we have, however, no data on the pineal eye or nostrils. The mouth was small. Impressions of gill chambers have been seen in *Thelodus*, but the nature of the external opening is unknown.

They have frequently been allied with the Heterostraci because of the similarities in body contours, but there is no proof of such association. Their scales are comparable to the superficial portion of the plates and scales of other ostracoderms. It was originally suggested that the coelolepids demonstrated a stage in the development of armor and that typical bony plates and scales might arise by a fusion and deeper growth of small and superficial structures such as those present here. But it seems more probable today that we here have indications of a degenerative process—a reduction of armor, which, if carried a bit further, would lead to the condition of isolated dermal denticles, as seen in sharks. While it is customary to regard coelolepids as ostracoderms, even this is uncertain. It is not impossible that they may be forerunners of some group of the later jawed fish types.

Primitive vertebrates.—In the previous chapter the problem of the history of skeletal materials—bone versus cartilage—was briefly discussed. Classical theory maintained that cartilage was the older material. But the paleontological data strongly suggest that bone was a primitive adult skeletal material, cartilage an embryonic adaptation which appears in the adult as the result of degenerative processes.

The evidence from the Agnatha tends strongly to support the latter view.

Modern jawless forms are boneless, those of the Silurian and Devonian all possess dermal bone, and in the cephalaspids there is, in addition, a well-developed internal bony skeleton. It may be argued that these ancient forms had still earlier cartilaginous forebears. If so, however, the time when bone was unknown must have been an exceedingly remote one, for bony tissues were present in the oldest vertebrate scraps from the Ordovician. If bone was a new invention among the older vertebrates, one would expect to find a progressive increase in ossification among the later representatives of the groups concerned. This, however, is the reverse of the true situation. In general, the later ostracoderms of the Devonian show a less substantial armor than that of Silurian forms; bone is regressive, not progressive, in its history among ostracoderms. As will be seen, a similar story of bone reduction is true of various other lower vertebrate groups.

It seems certain that in the ostracoderms we are dealing with a truly primitive series of vertebrate types. That the absence of jaws is a primitive feature need not be seriously questioned. This condition greatly limits the possible modes of life of primitive vertebrate types. The modern cyclostomes have been enabled to take up a predaceous mode of existence through the development of a rasping "tongue" as a substitute for jaws, and a type of nibbling may have been present in some ostracoderms. In general, however, the older vertebrates were limited, as to food supply, to tiny organisms and bottom detritus that could be strained through the gill apparatus, much as in lower chordates today. The gills, therefore, were not only a breathing, but also a feeding, device. In relation to this, we see that in most ostracoderms the major—anterior—part of the body was much expanded to form a large set of branchial chambers, surmounted by a brain and sense organs. Posterior to this, the trunk and tail appear as a relatively small locomotor appendage.

The modern cyclostomes lack paired limbs; among the ostracoderms we see various stages in the early development of paired-fin structures. Without such fins the locomotion of the oldest vertebrates must have been of the relatively ineffective and uncontrolled type seen in a frog tadpole. Paired flaps or rudders would aid greatly in preventing rolling and pitching and, if flexibility were attained, aid in steering. The finlike developments seen among the ostracoderms are not closely comparable to the "orthodox" fin structures of sharks or of higher bony fishes but presumably represent independent evolutionary developments. Similar essays in the establishment of paired-fin systems, often of curious types, will be seen among the placoderms. Paired fins, it seems probable, were developed in parallel fashion among various early vertebrates in relation to their needs for more efficient locomotion.

The ostracoderms are primitive vertebrates; but if we seek among the known forms for the ancestors of higher vertebrate groups, we meet with disappointment. The cephalaspids and anaspids show very definite characteristics (as in the development of nostril and hypophysis) which seem to ally them to the cyclostomes, and the anaspids especially may well be close to the cyclostome ancestry. It is, however, very improbable (although not impossible) that the ancestors of other vertebrate groups passed through a stage with the peculiar monorhine condition seen here.

The Heterostraci and coelolepids appear, in such features as their apparently diplorhine condition, to offer better prospects of relationship to higher vertebrates. We know, however, very little about the structure of the coelolepids, and the known Heterostraci are obviously too highly specialized in many ways to be considered in themselves as ancestors of any of the higher jawed vertebrates.

Our failure to find actual gnathostome ancestors among known ostracoderms is, of course, a result only to be expected from a broad consideration of the problem. The known forms are ancient vertebrates, it is true; but not the oldest of vertebrates. We know that the vertebrate stock was in existence a full period earlier, in the Ordovician; and it is possible that highly developed vertebrate types may have been in existence in the Cambrian, a hundred million years or more before the first adequately known types. Cephalaspids, anaspids, pteraspids, and coelolepids represent not the beginning but the end of a cycle of early vertebrate evolution—end-forms rather than generalized ancestral types.

The sea is generally assumed to have been the original home of life; lower chordates and lower living vertebrates are mainly marine types. It is, therefore, natural to believe that the vertebrates were originally dwellers in a salt-water environment.

This, however, is probably the reverse of the case. The active swimming characteristic of vertebrates suggests that their home lay in fresh waters where mobility was necessary to counteract the downward sweep of stream currents. Studies of kidney structures and function indicate that the primitive vertebrate kidney was one "invented" for use in a fresh-water environment and that this structure was variously modified by later marine types. The fossil record is in accord with these other lines of evidence. Nearly all records of Silurian and early Devonian vertebrates are of a type that suggests that the oldest fishes lived in inland waters. Most ostracoderms were apparently stream and pond dwellers; it is not until the later part of the Devonian that sharklike fishes and placoderms become numerous in the seas; few of the higher bony fishes appear to have been ocean dwellers before the Mesozoic.

Why should primitive vertebrates have been universally armored? Later armored types are usually protected against their own carnivorous relatives; but we believe that the earliest vertebrates were without biting jaws and incapable of ingesting other vertebrates as food. Obviously, the enemies must have lain among invertebrate types. The inland-dwelling vertebrate would not have come in contact with cephalopods or other marine forms which one might at first think of as possible enemies. We do, however, find that one group of predaceous invertebrates was present in the same beds with the early vertebrates—the eurypterids, aquatic, scorpion-like Paleozoic creatures of large size, with well-developed claws and biting mouth parts. It is probable that the early vertebrates furnished a food supply for the "water scorpions" and that vertebrate armor (and the electric organs of the cephalaspids) served as a defense against these carnivorous enemies. When, in the Devonian, faster-swimming fishes supplanted the comparatively sluggish ostracoderms, the eurypterids dwindled into insignificance and presently disappeared. The activity which characterizes the vertebrates may be related not merely to the taking-up of life in running streams but also to the necessity of escaping early eurypterid enemies.

CHAPTER 3

PLACODERMS

IN THE Devonian, often called the "Age of Fishes," we find present the ostracoderms, already discussed, and early representatives of the higher fish classes living today. A considerable majority of the fish population of that period, however, belonged to groups now long extinct and peculiar in structure: acanthodians, sharklike in superficial appearance but most unsharklike in anatomical features; the arthrodires, with heavy armor in articulated head and thoracic segments; the antiarchs, grotesque little creatures which look like a cross between a turtle and a crustacean; the odd stegoselachians, which are armored caricatures of modern skates and rays.

Where to place these seemingly aberrant forms was long a vexing problem. One or the other of these types has at times been thought allied to the ostracoderms, to the sharks, to the lungfish, to the "ganoids"; but in each case the supposed likenesses have been more than outweighed by the obvious differences. There are few apparent common features uniting these groups other than the fact that they are, without exception, peculiar. All, however, are characterized by the presence of bony skeletal tissues; all have paired fins, although they are built on unusual plans; and all have jawlike structures of some sort or other.

Jaws.—It is this last feature which provides a key to the position of these fishes and gives us grounds for uniting them in the class Placodermi, or plated-skinned fishes (Aphetohyoidea is an alternative term). They appear to represent the most primitive of gnathostomes, nature's first "experiments" in the production of jawed types.

We have earlier discussed, in brief fashion, the evolution of jaws. In most fishes, it was noted, the hyomandibular bone props the jaw joint against the braincase and thus aids in its support. In this condition the original gill slit between the jaw and the hyoid arch has been reduced to a small tube—the spiracle—distinct from the other gill slits and, if an operculum is present, opening separately to the surface of the body. It has long been assumed by anatomists that there must have existed a stage in vertebrate evolution in which jaws had been developed but the hyoid arch had not yet become specialized. No living fish remains in this stage. It has, however, become clear as the result of recent studies that this hypothetical ancestral condition was abundantly represented in the Paleozoic by the forms considered in this chapter. They are a series of bony fishes which had advanced over their ostracoderm ancestors in the development of jaws. In some cases, as in the acanthodians first to be described, the full jaw structure can be demonstrated, and the unspecialized nature of the hyoid arch is clear. In others our knowledge is less complete. Most, however, have an operculum or gill cover of some sort, and in none is there a separate opening for a spiracle. It is, therefore, a fair inference that in these forms the gill structure was similarly primitive in nature, with the hyoid arch and first gill opening in an unspecialized condition.

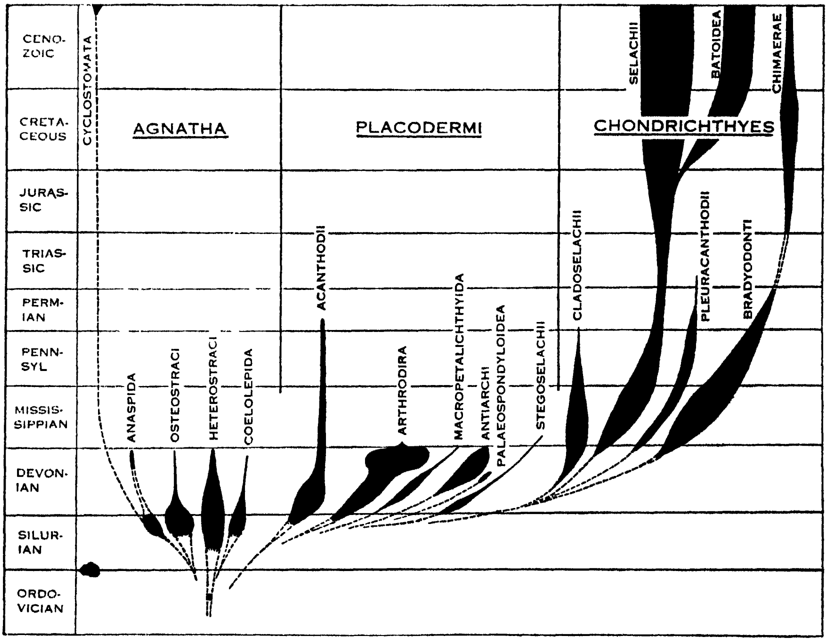


FIG. 23.—Diagram to show the evolution and distribution in time of the Agnatha, Placodermi, and Chondrichthyes.

The upper jaws, when developed, are always attached to the braincase or braced on it in some fashion. In placoderms this is done by a direct articulation of the palatoquadrate with the braincase. This condition is described technically as an autostylic one; a modification of it is seen in some higher types, in which (as in chimaeras, lungfishes, and modern amphibians) the upper jaw and braincase are firmly fused rather than merely articulated. With the development of an additional bracing by the hyomandibular there arises the amphistylic condition seen in primitive sharks (cf. Figs. 6, 55); if, as in later shark families, the entire jaw support is accomplished by the hyomandibular, the term hyostylic is applied.

Fins.—We have seen in the ostracoderms certain early essays in the development of paired fins in the shape of spines, flaps, or folds of some sort on either side of the body—structures which presumably aided in stabilizing the fish during progression. In the higher fish groups, above the placoderm level, appendages (unless secondarily lost or modified) invariably consist of two pairs, the pectoral fins in the "shoulder" region just behind the gill slits and the pelvic (or ventral) fins just anterior to the anal region; the pectorals are, in general, the more prominent of the two. Each fin articulates with a girdle of bone or cartilage, which lies inside the body wall and to which are attached muscles which move the fin. The pectoral girdle usually extends far up the flank and, in addition to internal cartilages or bones, may have, in bony fishes and land vertebrates, a covering layer of dermal bones; the pelvic girdle is less highly developed and typically consists of a small plate of bone or cartilage imbedded in the under surface of the abdomen.

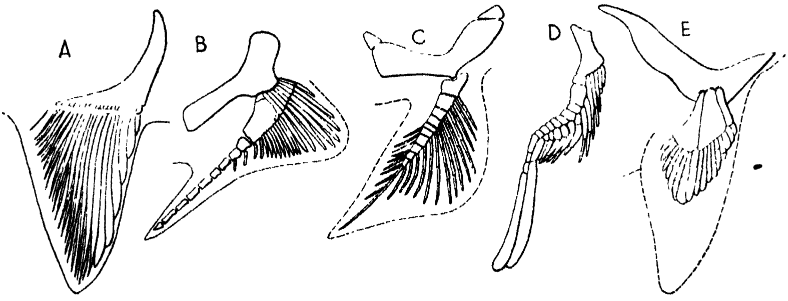


FIG. 24.—The paired fins and girdles of sharklike fishes. All except *D* are pectoral fins. *A*, *Cladoselache* of the late Devonian, with parallel radials extending out from the girdle; *B*, "*Cladodus*" *neilsoni* (Carboniferous), with a posterior axis developed, transitional between *A* and *C* or *E*; *C*, a pleuracanth shark, with archipterygial structure; *D*, pelvic fin of male of the same, with clasping organ; *E*, *Hybodus*, a Mesozoic shark. (*A* after Dean; *B* after Traquair and Goodrich; *C* and *D* after Fritsch; *E* after Smith Woodward.)

The nature of the fin itself is variable even in higher fishes; these variations may be illustrated by a consideration of fin types seen in sharklike forms (Fig. 24). One variety is a fin fold, a broad-based fin in which the skeleton consists of numerous parallel bars articulating with a longitudinal axial series of basal elements. Such a fin is seen in the oldest sharks, and a rather similar structure of parallel bars (although with a reduced number of elements) is found in the ray-finned bony fishes. A second type is that characteristic of modern sharks. Here the fin has a narrower base and greater flexibility, a condition presumably attained by swinging the basal axis outward so that only the anterior part of the fin attaches to the body. A third type, leaf-shaped, is seen in pleuracanth sharks, in which a long, jointed axis extends down the middle of the fin, with elements projecting from it on both margins. This structure (also seen in bony fishes related to tetrapod ancestors) has been named the archipterygium because of a theory that it is the original type of fin. It seems, however, much more likely that this is the reverse of the true situation and that it has evolved from a fin like that last considered; branching elements added behind the fin axis balance symmetrically those already present on the anterior margin of the fin. Distally, the substance of the fin may consist merely of a web of skin; usually, however, this web is reinforced by hard dermal structures in the shape of scales or horny rays.

Paired fins are generally present in placoderms. But, as will be seen, they are exceedingly variable in nature; in the case of fins, as of many other structures, the student of evolution who seeks generalized and diagrammatic ancestral types in these ancient jawed fishes is doomed to disappointment. An animal cannot spend its time being a generalized ancestor; it must be fit for the environment in which it lives and constantly and variably adapted to it.

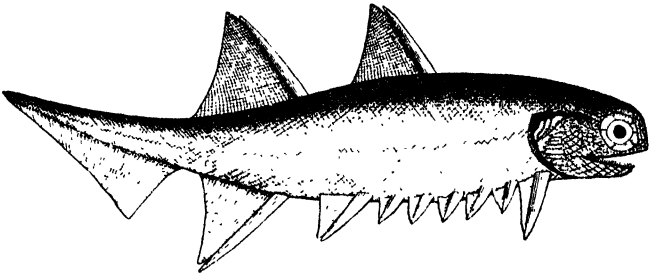


FIG. 25.—*Climatius*, a Lower Devonian acanthodian with accessory paired fins, about 3 inches in length. (Modified from Traquair and Watson.)

Acanthodians.—Least specialized of placoderms in general body features are the Acanthodii (Figs. 25–27), frequently but rather inaccurately termed "spiny sharks." These Paleozoic fishes are generally of small size, but a few inches in length, and usually found crushed flat in slabs of shale. Interpretation of their structure has therefore proved difficult. The acanthodians were superficially sharklike in their proportions and in the presence of a heterocercal caudal fin. This fin type, however, appears to have been the general primitive one in all fishes above the placoderm level, and in other characteristics the acanthodians show little specific resemblance to the selachians. They are covered, not with isolated dermal denticles as are sharks, but with a complete armor of true scales, composed of bonelike material, diamond-shaped and of small size. A scaly covering was characteristic of most ostracoderms and hence appears to be a primitive feature. It is of interest that the microscopic structure of the acanthodian scales is almost identical with that of the ganoid scales found in many higher bony fishes (cf. Fig. 61) which appeared at a later time. Larger dermal plates, sometimes in a complex pattern, may be present in the shoulder region.

The head is covered by a continuation of the dermal armor of the body. Here we find a series of small plates, arranged in definite patterns but not forming large bony elements or a shield (except for a prominent ring about the orbit). This is in contrast to the heavier armor found in most other Paleozoic vertebrates (sharks excepted). The gill region appears to have been covered, as in jawed fishes other than sharks, by opercular structures, presumably folds of skin reinforced by small dermal plates or scales. This covering, however, seems to be of an unusual nature. In the higher fish groups the operculum, when present, grows backward from the region of the hyoid arch, leaving the spiracle to open freely in front of it. Here each gill appears to grow a small flap, but the main operculum—stiffened by parallel bony bars or rays—grows back from the posterior margin of the jaws and covers the whole gill series. This suggests that the first slit still resembled those behind it—a suggestion confirmed by the internal structure.

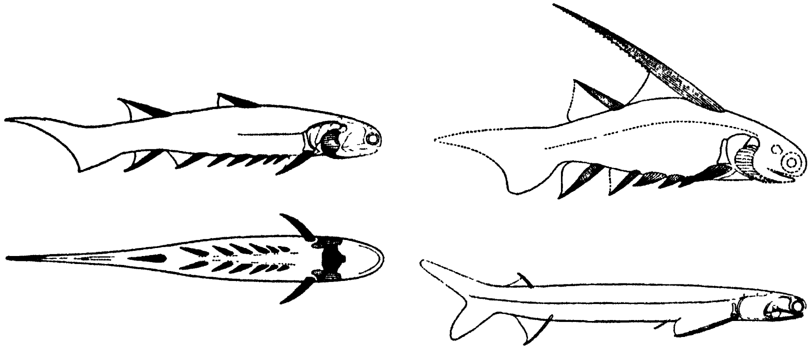


FIG. 26.—Outline drawings of various acanthodians. *Left,* lateral and ventral views of *Euthacanthus* of the Lower Devonian with five supernumerary pairs of fin spines; original about 6 inches long. *Upper right, Parexus,* a Lower Devonian form about 5 inches long, with large dorsal fin spines. *Lower right, Acanthodes* of the Permian, an elongate and apparently degenerate type reaching a foot in length. (From Watson.)

The fins are of an unusual type. All, except the caudal, are stiffened anteriorly by dermal spines, sometimes of considerable size. In many cases only the spines are visible in the material; in others, however, there is evidence of a true fin structure. This consists primarily of a web of skin attached to the spine; occasionally there are traces of an internal skeleton in the fin and of tiny scales covering its surface. Of median fins there are one or two dorsals and an anal. Of paired fins there are always readily distinguishable pectorals and pelvics in normal position. Most acanthodians, however, exceed this number and have additional smaller spine pairs between the major ones—in one genus as many as seven pairs of spines are present (Fig. 25).

Owing to the small size and crushed type of preservation of the material, we know little of the internal structure of acanthodians. The postcranial skeleton is quite unknown in most forms; in a few cases vertebral ossifications have been observed. The internal skeleton of the head and gill region is adequately known only in *Acanthodes* (Fig. 27), which is, unfortunately, a late and (we suspect) rather degenerate genus.

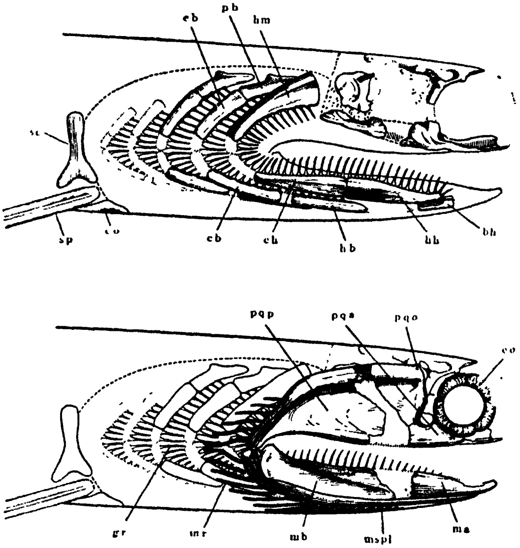


FIG. 27.—The skeleton of the head and gill region of *Acanthodes*. In the lower figure the superficial dermal plates and scales have been removed (except for a circumorbital series, *co*), but all deeper structures are shown. Jaws comparable in many ways to those of sharks (cf. Fig. 55) are present, but the upper jaw is ossified in three pieces (*pqo*, *pqa*, *pqp*), the lower jaw in two (*ma*, *mb*), while the latter is braced by a splintlike dermal bone (*mspl*). Rays (*mr*) extending back from the jaws presumably supported an operculum.

In the upper figure the jaws are removed to show the underlying structures. The braincase includes a number of ossified areas. The hyomandibular (*hm*) appears to have had no contact with the jaws, and the presence on the hyoid arch of a comblike series of gill rakers comparable to those of other gill arches (*gr*) indicates that a fully developed gill slit lay between jaws and hyoid arch. Abbreviations: *hm*, *ch*, *hh*, *bh*, elements of hyoid arch—hyomandibular, ceratohyal, hypohyal, basihyal; *pb*, *eb*, *cb*, *hb*, elements of more posterior branchial arches—pharyngobranchial, epibranchial, ceratobranchial, hypobranchial; *sp*, *sc*, *co*, spine of pectoral fin and elements perhaps homologous to the scapula and coracoid of the shoulder girdle in bony fishes and tetrapods. (After Watson.)

A considerable part of these structures was well ossified. There appears to have been a braincase of fairly normal fish build. This was ossified to a variable degree; in *Acanthodes* there were several bony regions separated by areas in which ossification was feeble or lacking. The orbits were large, the snout very short, the nostrils close together near the tip of the snout—features quite unlike those of sharks but comparable to those of ray-finned bony fishes. Upper and lower jaw bars were present and closely comparable in shape to those of Paleozoic sharks (cf. Fig. 55). In some genera there is but a single ossification in each jaw element; in *Acanthodes*, however, the palatoquadrate ossifies in three portions, the lower jaw in two. The mandible is braced by a splintlike dermal bone. The jaw is articulated with the braincase anteriorly, and, in some cases at least, there is a well-developed articulation with a postorbital process, as in early sharks. The teeth are variably developed; they are seldom present on the upper jaw, and *Acanthodes* was toothless. The replacement teeth in each series are sometimes seen to form little whorls, as in many sharks (cf. Fig. 48), and there may be an especially prominent median whorl at the jaw symphysis.

Back of the jaws is found a series of five well-developed gill arches. The last four are normal fish structures; the first, which obviously corresponds to the hyoid arch, lacks much of the specialization seen here in higher fish types. Its upper portion, corresponding to the hyomandibular, is a single rather than a jointed element and is somewhat enlarged. But it appears not to have attached to or supported the jaws; and the fact that this arch, like those behind it, bears on its inner margin a strong series of gill rakers indicates that a fully developed gill slit, rather than a spiracle, was present between jaws and hyoid arch. Thus we have in *Acanthodes* the relatively unspecialized type of jaw apparatus which is expected by theory in a primitive gnathostome.

The acanthodians are apparently the oldest of known groups of jawed vertebrates. No complete skeletons are known from the Silurian, but bone beds of that period yield a wealth of spines and scales which appear to be acanthodian in nature. In the Lower Devonian the group had already reached its peak in numbers and variety, and acanthodians are one of the most abundant of vertebrate groups in fresh-water deposits of this age. *Climatius* (Fig. 25), *Euthacanthus*, and *Parexus* (Fig. 26) are representative primitive genera. The body was rather short and deep; the fin spines are large—particularly so in *Parexus*—and from three to five pairs of extra fins were present. In other genera of this age, however, the body tends to be rather more elongate and the fin spines more slender, and there is little development of extra fins. Beyond the Lower Devonian, acanthodians are relatively rare (perhaps because of the competition of higher bony-fish types then abundant). They are present, however, in many Carboniferous localities. The last of the group is *Acanthodes* (Fig. 26) of the European Lower Permian, a rather degenerate type, with an elongate, somewhat eel-like and partially scaleless body and a toothless mouth.

The more typical acanthodians were small fresh-water dwellers. It is probable, however, that some of the acanthodians went to sea, as did other fish groups in the Devonian and Carboniferous, and there developed into forms of large size. In late Paleozoic marine deposits there are frequently found isolated spines, usually classified by paleontologists as ichthyodorulites. Most were presumably carried by sharklike fishes higher in the evolutionary scale; others, however, may have pertained to acanthodians. This seems certainly true of *Gyracanthus*, a name given to a common type of large Carboniferous fin spine. In the Middle Devonian seas lived *Onychodus*, known mainly from large dermal jaw plates containing pointed marginal teeth and with a whorl of large teeth between the two halves of the jaw; its status is uncertain, but it may well have been a specialized acanthodian.

This order of early fishes shows an interesting combination of primitive and seemingly specialized features. The general structure of the jaw and gill-arch apparatus is, we may believe, a truly primitive one, from which the more advanced condition seen in sharks, for example, might be readily derived. In view of our present knowledge of fish evolution, the presence of internal bony structures in primitive jawed fishes is not surprising. In some respects, at least, the nature of the paired fins—particularly their variable number—is suggestive of primitive conditions. The acanthodians were at a stage when vertebrates had not, so to speak, made up their minds as to how many fins were the proper number.

In other respects the acanthodians show features which are less clearly primitive and which in some cases may well be aberrant. The prominence of spines in the paired-fin structures seems, at least at first sight, a specialization. But it will be recalled that cephalaspids and anaspids among jawless vertebrates show paired spines which may be the forerunners of paired fins; other placoderms, as we shall see, show even greater spiny developments; the dorsal fins, at any rate, bore spines in primitive sharks. Possibly spine outgrowth may have been the initial stage in the evolution of paired fins; the appearance of a fin membrane behind the spine and its elaboration into a typical fin may have been subsequent stages in limb evolution.

A still greater objection to the acanthodians as ancestors of more progressive fishes appears to be the development of an operculum which, unlike that of higher bony fishes, covers the spiracular region. But this operculum appears to have been variable among acanthodians and may not have been present in the ill-known Silurian types. Apart from this feature, the acanthodians apparently are forms which might well be close to the line of descent of higher fishes.

Arthrodires.—The arthrodires—jointed-necked fishes—are a group of Devonian placoderms much more prominent than the acanthodians but apparently much more aberrant and destined to speedy extinction and phylogenetic sterility. These forms were characterized by the presence of a bony armor composed of two parts, one covering the head and gill region and the second inclosing much of the trunk, the two connected by a pair of joints. Peculiar bony jaws were present, and there were paired fins of some sort in many forms, at least. These features are well shown in such typical arthrodires as *Coccosteus* (Figs. 28, 29) and *Dinichthys* (Fig. 30). The former was a Middle and Upper Devonian fish of modest size, reaching perhaps 2 feet in length, the latter, a giant late Devonian type; but, except for some features suggesting reduction in the dermal armor in the latter, the two were essentially similar in known structures.

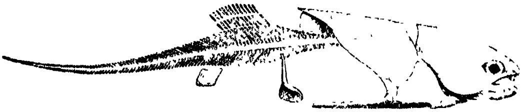


Fig. 28.—*Coccosteus*, a small arthrodire of the Middle and late Devonian, with reduced pectoral spines; original about 16 inches long. (From Heintz.)

The body appears to have been of fairly normal fish shape, although rather broad and flat. The posterior region is adequately known only in *Coccosteus*. Scales or denticles have been found in but a few instances, and the skin may have been smooth and naked in most arthrodires. No trace of vertebral centra has been discovered, but there were well-ossified neural and haemal arches. The column tilted up at the posterior end, suggesting the presence of a heterocercal tail. A series of cartilages above the backbone indicates the presence of a dorsal fin, while a ventral plate presumably supported an anal.

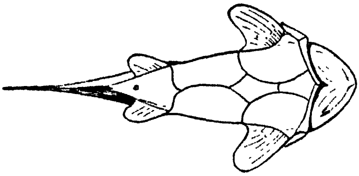


Fig. 29.—A ventral view of *Coccosteus*, with paired fins restored. (From Heintz.)

The armor plates were of bone, often ornamented superficially by dermal denticles, and comprised a complex series of median and paired elements, which were, in general, uniform in number and position throughout the group. These plates cannot be homologized satisfactorily with those of higher bony fishes, and a special series of names, noted in Figure 30, are applied to them. Grooves in the surface of the plates indicate the presence of a well-developed lateral-line system. (The head shield consisted of a series of plates covering the top and sides of the cranial and gill regions. Large paired orbits were present and a pineal eye as well, although this often failed to pierce the armor and reach the surface. A sclerotic ring of thin, bony plates was present in the eyeballs. This protective structure, found in many higher bony fish and tetrapods, in arthrodires consisted of four elements.) In some cases notches at the anterior end of the shield mark the position of paired nostrils. These are placed close together, and, as in acanthodians, there is no development of the rostrum seen in sharklike fishes. Most of the head plates were firmly united, but the plates beneath and behind the eyes and over the gill region were but loosely attached to the roofing bones in advanced members of the group.

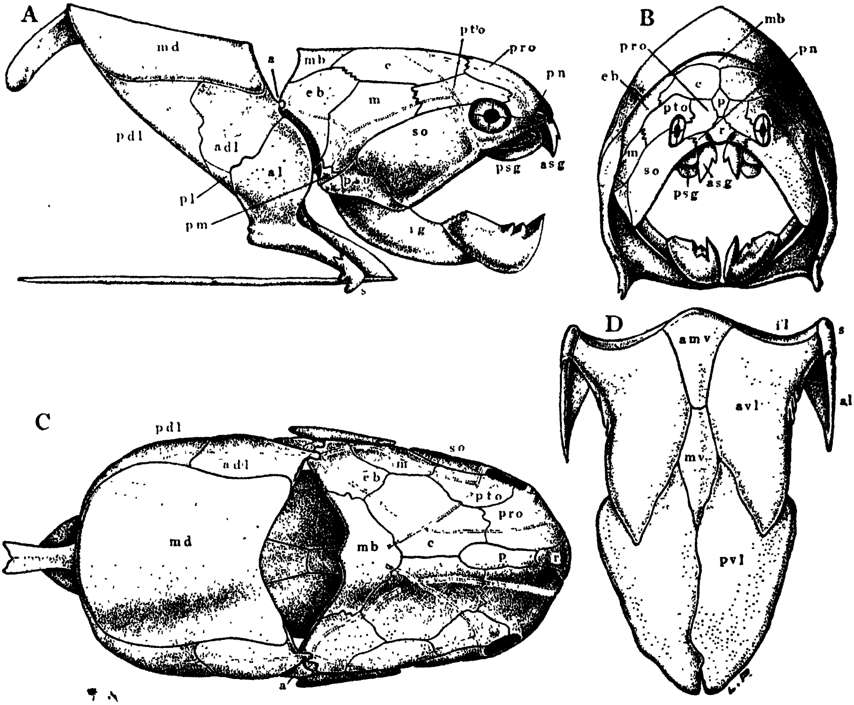


FIG. 30.—*Dinichthys. A*, Lateral, *B*, anterior, and *C*, dorsal view of armor; *D*, ventral shield. Mainly based on the large *D. terrelli* in which the armored region is about 10½ feet long. Lateral-line canals are indicated. The dermal plates of arthrodires cannot be readily homologized with those of other vertebrates and have been given a series of arbitrary names, listed below with their abbreviations: *a*, joint between head and thoracic shields; *adl*, anterior dorsolateral; *al*, anterior lateral; *amv*, anterior median ventral; *asg*, anterior supragnathal; *avl*, anterior ventrolateral; *c*, central; *eb*, external basal; *ig*, inferognathal; *il*, interlateral; *m*, marginal; *mb*, median basal; *md*, median dorsal; *mv*, median ventral; *p*, pineal; *pdl*, posterior dorsolateral; *pl*, posterior lateral; *pm*, posterior marginal; *pn*, postnasal; *pro*, preorbital; *psg*, posterior supragnathal; *pso*, postsuborbital; *pto*, postorbital; *pvl*, posterior ventrolateral; *r*, rostral; *s*, spinale; *so*, suborbital. (After Heintz.)

The jaws were very peculiar in structure. In most cases the upper jaws are represented only by two pairs of elements, the front pair usually having a sharp tusklike projection, the posterior bearing a long shearing edge. Below, a single long element bearing a "tusk" in front and a shearing edge farther back was present on either side. These structures were very different from the jaws of normal fishes. The projections seen in the adult were not teeth but simply hard bony surfaces; in some cases young forms possessed pointed toothlike structures fused to the jaw bones. There was seldom any bony connection between the different parts of the jaw apparatus or between upper-jaw bones and the head plates. It is obvious, however, that these jaw elements are dermal ossifications which must have been attached to deeper-lying structures corresponding to the upper- and lower-jaw bars—the palatoquadrate and the mandible. In most instances these elements appear to have remained cartilaginous; in a few, however, they have been preserved in a partially ossified condition.

In most of the typical arthrodire genera no traces of the braincase have been found, although rugose surfaces and projections for its attachment are found on the under side of the skull roof. Some partially ossified specimens are, however, known; and data from more primitive arthrodires in which ossification was more thorough show that a broad and massive braincase was present, comparable to that of other fish groups in general structure although differing much in details.

It is certain that the posterolateral portions of the head shield covered the gill chambers and that these areas of the shield functioned as an operculum; the gills (as in bony fishes) thus had a common opening to the surface through the slit between the head shield and that portion of the trunk armor which lies in the position of a shoulder girdle. No trace of the gill structures has ever been described. We may note, however, that arthrodires lack a spiracular opening and reasonably infer that the first gill slit—and hence the hyoid arch—was unspecialized, as in acanthodians.

The thoracic armor entirely surrounded the body. Dorsally on either side it articulated with the head shield by complicated peg-and-socket joints, indicating that there was a habitual movement of the head on the trunk. It is possible that in arthrodires (in contrast with other vertebrates in which the head remains fixed and the lower jaws move) the lower jaws may have remained relatively stationary in feeding and the head moved up and down on them. The thoracic armor, both above and below, extended far back over the trunk region; and, below, it also extended some distance forward to protect much of the throat. The somewhat arched dorsal shield and the flattened ventral plate were composed of a number of closely connected elements with a nearly uniform arrangement in all typical members of the order. The lateral bony elements connecting the dorsal and ventral shields were situated in what is obviously the shoulder region and have been compared with the dermal bones in the same situation covering the pectoral girdle in the Osteichthyes.

From the sides of the shoulder region projected a fixed bony spine, fairly long in *Coccosteus*, vestigial to absent in later and larger types. This spine was in the position of the pectoral fin in more normal fishes. There is evidence indicating that a pectoral fin, supported by short radials, was present behind the spine in *Coccosteus* (Fig. 29). Behind the shield region a plow-shaped bone represents a pelvic girdle; in exceptional instances traces of small (and spineless) pelvic fins have been found associated with it.

Coccosteus was fairly common in the Middle Devonian and probably ranged from fresh to brackish waters, showing a tendency toward a marine life. A number of related but highly varied forms, all comparatively small and well-armored types, have been found in the lower part of the marine Upper Devonian of Germany. They varied widely in proportions—some were very broad-headed, others had much elongated snouts, for example—and are arrayed in a number of distinct, although related, families. One genus (*Synauchenia*) shows a remarkable feature in the complete fusion of head and shoulder shields. In the late Devonian the arthrodires, then seemingly inhabiting brackish to salt waters, reached a climax in size and numbers. A great assemblage of types has been recovered from the black shales of the Cleveland region. Most common is *Dinichthys*, which reached a length estimated at 30 feet. In this giant type, in contrast with *Coccosteus*, the armor was shortened, on both the head and the trunk; the shoulder spine was tiny or absent; an unprotected gap developed between the two shields; and the bones tended to be proportionately thinner and more loosely attached to one another. These changes were also present in great measure in a number of other contemporary forms. Some were smaller than *Dinichthys*, but *Titanichthys* was even larger, and the average size had greatly increased since Middle Devonian days. The jaw apparatus varied considerably; *Mylostoma* had even developed crushing plates for mollusk-eating. In all, however, a reduction in the area covered by the armor and a reduction in its relative (although not absolute) thickness seems to have occurred with increase in size and tendency toward a marine life. This late Devonian climax marks the end of the group, for no arthrodires survived into the Mississippian.

Early arthrodires.—*Arctolepis* (Fig. 31) and *Phlyctaenaspis* are representative of a group of small and early arthrodires. These are mainly Lower Devonian fresh-water types, and there even appear to be traces of such forms in the late Silurian. They are thus among the oldest of gnathostomes. The arctolepids had a head shield much like that of later arthrodires but with the eyes far forward; plates bordering the mouth have never been discovered. The stout thoracic shield was elongated and rather flat, and only in seemingly advanced forms are there indications of a division into separate elements. The trunk armor extended nearly as far back at the sides as it did above and below, whereas in forms from the late Devonian upper and lower shields were almost separate. The bones comprising the armor are fused with one another, and sutures are rarely seen. A conspicuous difference from later types was that, instead of small spines at the side of the shoulder region, there were long, hollow, curved cone-shaped projections of the armor. These fixed structures would have been a hindrance rather than a help in swimming; the rather flat build of these fishes suggests that they were bottom-living forms, and these winglike projections may have been of use in wriggling upstream against a current. Little is known of the posterior part of the body; there is, however, evidence suggesting that, in contrast to later arthrodires, scales may have been present.

Aberrant arthrodires.—The forms so far described are such as appear to comprise the main line of arthrodire evolution. From this there were, however, many divergent branches during the Devonian. Some of these consist of forms in which the body tended to assume a depressed shape, giving rise to sluggish bottom dwellers. *Holonema* is representative of a family in which the body was moderately depressed and the trunk armor much elongated. *Homostius* (Fig. 32) and *Heterostius* are much more flattened, but with a different type of specialization of the armor. The head shield is greatly elongated posteriorly, suggesting an expansion of the gill chambers; the pectoral armor, on the other hand, is quite short dorsally, although the ventral elements of this series extend far forward beneath the head. The jaws were weak and slender; as in advanced arthrodires the pectoral spines were lost. These forms grew to large size. They appear to have lived in brackish estuarine waters, and are frequently found in the Baltic region in later Devonian deposits, which appear to be of this origin. A still more peculiar depressed type is *Phyllolepis* (Fig. 34), common in the Upper Devonian and readily rec-

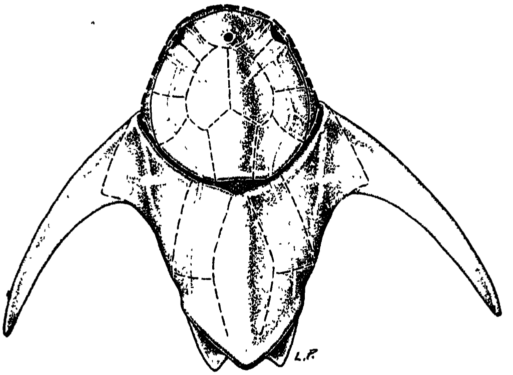


FIG. 31

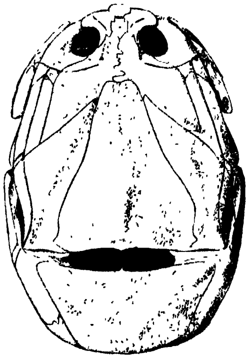


FIG. 32

FIG. 31.—Dorsal view of *Arctolepis*, a primitive arthrodire with enormous pectoral appendages. The jaw elements are unknown. (After Heintz.)

FIG. 32.—Dorsal view of the armor of *Homostius*, a large flat-bodied arthrodire with long cranial and short trunk armor. (After Heintz.)

ognized by its plates, which are ornamented with fine concentric lines. This form was so depressed and featureless that it was long thought to be an ostracoderm allied to *Drepanaspis;* and it is only recently that it has been recognized as a degenerate arthrodire which has lost much of its head armor except for an enlarged median element. The thoracic armor, with stout pectoral spines, persisted, however.

Ptyctodonts.—The name *Ptyctodus* has been applied to small bony plates, often no larger than a date pit, found in late Devonian deposits. Usually a hardened area is to be found on one surface, suggesting that they were grinding jaw plates of a small fish of some sort. It was once thought that they pertained to chimaeras, sharklike types with somewhat similar tooth plates; but these forms appear much later in geologic history. Some Devonian ptyctodont plates were much larger and more like those of arthrodires, and in *Rhamphodopsis*, a related genus (Fig. 33), skeletal remains are known. It is clear that we are dealing here with arthrodires, although arthrodires of a rather peculiar type. The posterior part of the body was naked except for a few scales above the heterocercal caudal fin; one, perhaps two, dorsals were present; a pelvic girdle and a scale-covered pelvic fin occur rather far forward on the body. There is a set of thoracic armor plates in the shoulder region, comparable in general construction to those of normal arthrodires but rather narrow. Laterally, there is a large pectoral fin spine like that of primitive arthrodires. Dorsally, the shoulder plates support a large spine, which may have acted, as in acanthodians, as a cutwater for an anterior dorsal fin.

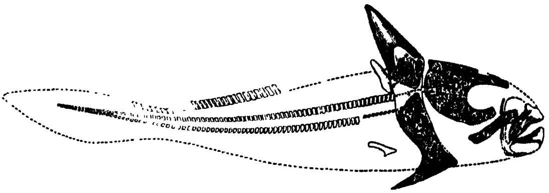


FIG. 33.—*Rhamphodopsis*, a ptyctodont arthrodire, about natural size. (After Watson.)

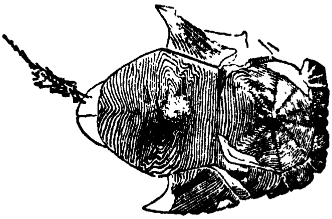


FIG. 34.—*Phyllolepis*, a degenerate late Devonian arthrodire about ¼ natural size. (From Smith Woodward.)

The shoulder armor articulates with a head shield comparable in part to that of normal arthrodires, but much reduced in extent. In the mouth lay stout upper and lower dental plates. The upper and lower jaw bars, to which the plates were attached, were partially ossified and were preserved, although imperfectly. Of great theoretical interest is the fact that the hyoid arch elements have been identified as a set of slender bones which obviously played no part in jaw support—the placoderm condition, which is assumed to be present in all arthrodire types.

The structures seen in *Rhamphodopsis* indicate clearly that in the ptyctodonts we are dealing with a somewhat aberrant group of arthrodires which had taken to eating mollusks or some other type of hard invertebrates as food. In most respects it is not difficult to derive the ptyctodonts from the arctolepid arthrodires. The only unusual feature is the large dorsal spine. This is suggestive of a fin spine of the type seen connected with acanthodian dorsals; the pectoral spines, too, resemble those of acanthodians much more closely in their shape and ornamentation than do those of other members of the order. Possibly very early arthrodires bore spines on other fins than their pectorals and thus resembled the acanthodians more closely than do characteristic arthrodire genera.

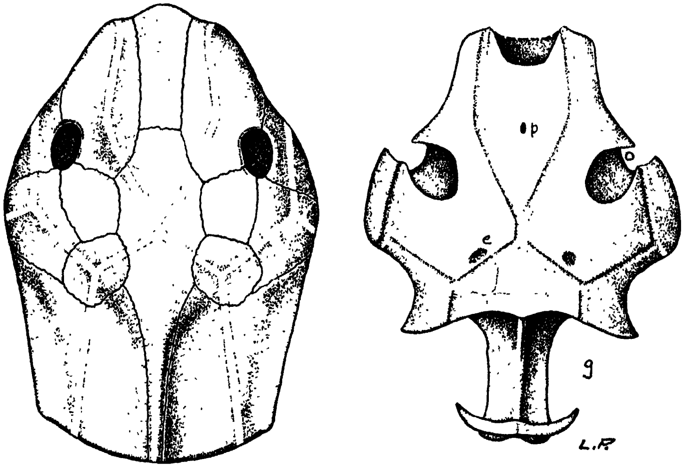


FIG. 35.—*Macropetalichthys*, an armored Devonian form related to the arthrodires. *Left*, dorsal view of head armor; *right*, the underlying braincase. The position of the lateral-line canals is indicated. Abbreviations: *e*, opening of endolymphatic duct from inner ear; *g*, position of gill chamber beneath lateral back corners of shield; *o*, orbit; *p*, pineal. Original about 9 inches long. (After Stensiö).

Macropetalichthys.—The genus *Macropetalichthys* (Fig. 35) has been known for a century from head shields found in various marine formations of Devonian age. This shield is rather generally comparable to that of arthrodires, although there are differences in the arrangement of its component plates. Beneath this shield there have been found in a few specimens remains of the partially ossified braincase, from which much of the structure of the head, including brain, nerves, and blood vessels, has been made out. This structure lay below the anterior two-thirds of the bony head shield;

posteriorly an extension ran back to connect with the front end of the vertebral column, while cavities containing blood vessels show that the gills were located under the back part of the shield on either side. The braincase is very broad and resembles that of the arthrodires, as far as they are known.

Until recently no further remains of *Macropetalichthys* had been identified. We now know, however, that behind the head shield this fish carried a set of thoracic plates with large pectoral spines very similar to those of arctolepid arthrodires. In a related Lower Devonian genus, *Lunaspis* (Fig. 36), the entire body has been recovered; unlike the arthrodires, the body of this fish was completely covered by large scales. It is obvious that the *Macropetalichthys* group is closely related to the arthrodires, with comparable armor. But the presence of body scales is a feature (presumably primitive) not seen in that group. And a lack of well-formed articulations between head and thoracic girdle, differences in plate arrangements of the bony elements, etc., suggest that it is perhaps better to place these forms in an order separate from (although related to) the arthrodires themselves.

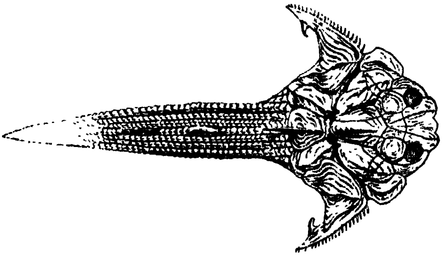


FIG. 36.—*Lunaspis*, a Lower Devonian member of the *Macropetalichthys* group, seen in dorsal view; the armored region is crushed flat and the width hence exaggerated. (After Broili and Gross.)

Antiarchs.—Likewise related to the arthrodires but even more specialized were the members of the order Antiarchi, small but abundant Devonian fresh-water forms. The first representatives of the group are found in Middle Devonian strata where *Pterichthyodes* [*Pterichthys*] (Figs. 37, 39) and *Asterolepis* are the common types, while, in Upper Devonian deposits, *Bothriolepis* (Fig. 38) is very numerous; the group disappeared without leaving any descendants in rocks of later times.

The posterior portion of the trunk and tail was rather normally fishlike in appearance, scaled in *Pterichthyodes* but naked in *Bothriolepis*, with a heterocercal caudal and one or two dorsal fins. The anterior portion of the body was covered with an armor structurally similar to that of arthrodires and similarly divided into head and trunk portions. The under side of the solid box formed by the armor was flattened, but the thorax was arched, with a decided peak at the top. The head shield was quite short and composed of a number of plates not readily homologized with those of arthrodires. The two orbits, with the pineal eye between them, were situated close together on the top of the head and directed upward. This gave an appearance somewhat like that of *Cephalaspis* but only indicates that we are again dealing with bottom-living fishes. The nostrils were placed close together on the upper surface of the shield not far in front of the eyes. The preserved jaw parts consist of small transversely placed plates of bone even more aberrant in appearance than those of arthrodires. The gills were located under somewhat movable plates at the back corners of the head shield. The arrangement of the elements of the body shield was quite similar to that found in primitive arthrodires and suggests a close relationship to those forms. Apparently this shield extended nearly the full length of the trunk.

In some specimens traces of soft internal structures have been preserved. It is certain that the intestine resembled that of sharks, dipnoans, and other primitive fish types in containing a characteristic spiral valve. Of great interest are distinct traces of a pair of large sacs connected with the floor of the pharynx. These can be interpreted only as lungs. Such structures, we believe, were present in early bony fishes of all sorts, but they are absent in sharks and have been thought to be a relatively late development in fishes. The evidence from the antiarchs suggests, however, that they may have arisen at a much lower stage in vertebrate evolution than had been suspected.

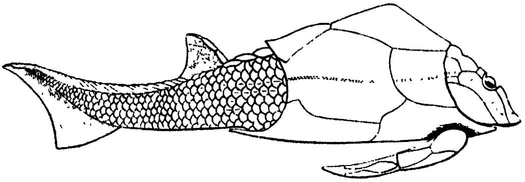


FIG. 37.—*Pterichthyodes* [*Pterichthys*], a scale-covered Middle Devonian antiarch, original about 6 inches long. (After Traquair.)

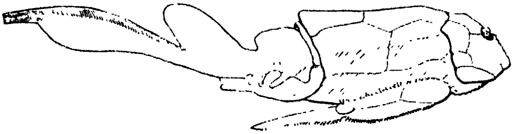


FIG. 38.—Lateral view of the Upper Devonian antiarch, *Bothriolepis*, a form with a scaleless trunk and tail. (After Patten and Goodrich.)

Folds of skin found at the posterior end of the trunk shield in *Bothriolepis* may represent pelvic fins, but this is doubtful. In the shoulder region we find, as we do in primitive arthrodires, prominent projecting bony structures. But in arthrodires these projections are fixed spines; here they are freely movable appendages composed of a large number of plates, with more the appearance of arthropod limbs than those of a normal vertebrate. Internal skeletal structures are present in the proximal part; there is a well-developed articulation with the shoulder region and (except in one instance) a second joint halfway toward the pointed tip.

These small fishes appear to have been bottom-living forms, perhaps crawling about with their peculiar flippers more than swimming. With their small mouths and weak jaw apparatus they presumably fed either on small invertebrates or on soft vegetation. The antiarchs are surely related to the arthrodire stock but have become even more specialized than have the members of that remarkable order.

Stegoselachians.—The ordinal term Stegoselachii—"armored sharks"—is used here as a heading under which to discuss a small series of unusual Devonian fishes, most of them recently discovered and poorly known. All the specimens are from salt- or brackish-water deposits, and most of them from the Lower Devonian of the Rhine region; they appear to represent one of the earliest movements of vertebrates into a marine environment. Because of their unusual characters and the rarity of their remains, they are very difficult to place. Their general appearance suggests that of the skates and rays. This resemblance can, however, be but a superficial one, for the stegoselachians far antedate these modern forms. The surface of the skin is denticulate, but over much of the body there are armor plates and scales, to which these denticles were attached. The gill chambers were covered; there is no evidence of a separate spiracular opening; and the jaws appear to have been short and probably lacked hyoid support. Presumably, then, we are here dealing with a group of placoderms, despite the great difference in appearance from the orders previously described.

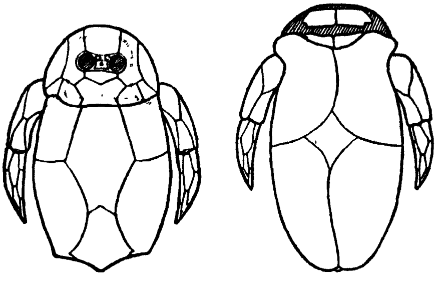


FIG. 39.—Dorsal and ventral views of the armor of *Pterichthyodes*. The elements of the thoracic armor are comparable to those of arthrodires (cf. Fig. 30). (After Traquair.)

Gemuendina (Fig. 40) is the best-known member of the group; a number of specimens have been found in the Lower Devonian of the Rhineland. The body was broad; the extraordinarily developed pectoral fins, supported by a series of long radials, give the creature a very skatelike appearance. Pelvic fins of more modest size were present, and beyond this a tapering tail covered with rows of scales. A small spine marks the position of a single dorsal fin.

The body is, for the most part, covered superficially by a series of star-shaped tubercles which have the appearance of sharklike dermal denticles. Closer study, however, shows that these are not separate structures but the surface of dermal plates. Over much of the body and portions of the head these plates are tiny mosaic elements; larger plates are, however, present anteriorly. A median head plate covers the braincase, and there are several paired lateral cranial elements. In the shoulder region the structure is difficult to determine, but there is a set of broad pectoral plates comparable in a general way to those of arthrodires.

The eyes faced dorsally and were placed close together on the top of the flat head, and the paired nostrils were likewise dorsal in position; the arrangement of these sensory structures superficially resembled that of antiarchs. The mouth was terminal and armed with stellate and pointed teeth resembling the tubercles of the body covering. Gill chambers presumably occupied much of the lateral regions of the "head."

The ossified braincase (better preserved in related forms from the later Devonian) was a relatively long and slender structure, contrasting in shape with that of arthrodires. There was a well-developed articulation with the vertebral column; this last structure is unusual in that it appears to have had well-ossified centra for at least part of its length.

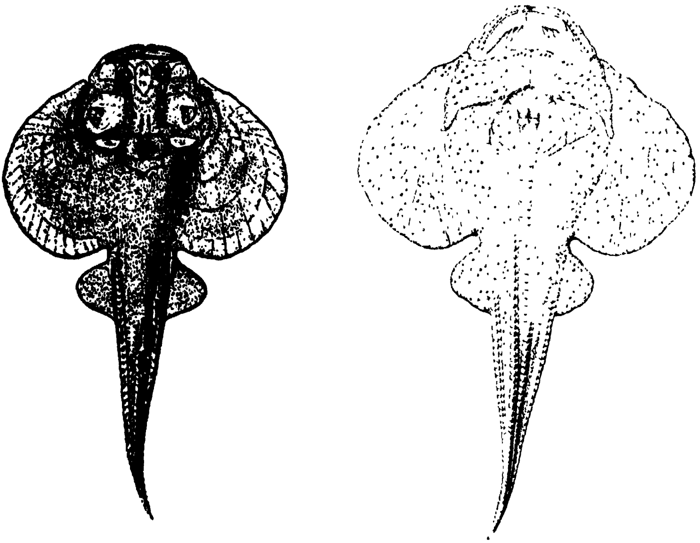


FIG. 40.—Dorsal and ventral views of *Gemuendina*, a Lower Devonian skatelike stegoselachian. Original about 9 inches long. (After Broili.)

Several other specimens from the same Lower Devonian deposits are of fishes which appear to be of a somewhat similar nature. *Stensioella* (Fig. 41) is known from a single specimen seen in dorsal view. It has a tubercular skin covering and a plate-covered head region, as in *Gemuendina*, and well-developed, fan-shaped pectoral fins are present. But these fins are much smaller than those of *Gemuendina;* the eyes are more lateral in position; the nostrils do not appear on the roof of the skull; and there is no evidence of pelvic fins.

Pseudopetalichthys (Fig. 42), from the same beds, appears to be a similar fish, seen from the ventral side. There are pectoral and pelvic girdles and the skeletons of paired fins, which might have been quite similar to those of *Gemuendina* or *Stensioella.* Ossified gill bars and peculiar broad, short jaws are preserved; there is no evidence of support by a specialized hyomandibular.

The stegoselachian skeletons just described are all from the Lower Devonian. In later marine rocks of that period there are a few fragmentary remains of forms related to *Gemuendina;* in the early Mississippian a single imperfect specimen perhaps represents a final member of the order.

Our knowledge of the group is far from satisfactory, and its position in fish history is debatable. However, the jaw structures appear to be primitive and in the placoderm grade of development; the presence of head and shoulder armor suggests relationships with the more heavily armored placoderms. Not improbably the stegoselachians were placoderms in which spiny appendages had been lost, armor was undergoing reduction, and the development of fins was greatly accelerated. Some further reduction in the hard skeleton would produce very sharklike types. These odd fishes may not be shark ancestors, but they closely parallel the conditions which we should expect in the ancestry of that probably degenerate group.

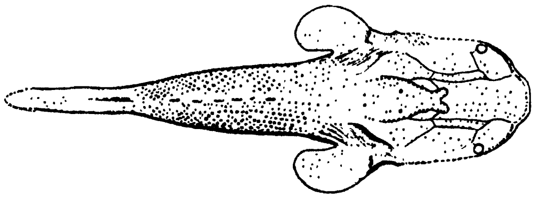


FIG. 41.—Dorsal view of the stegoselachian *Stensioella;* about ⅓ natural size. (From Broili.)

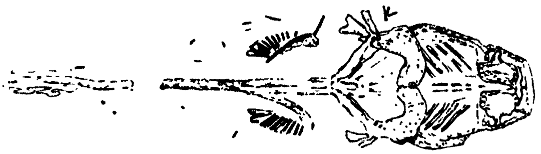


FIG. 42.—Ventral view of *Pseudopetalichthys,* a stegoselachian, about half natural size. Beneath the head region are seen peculiar jaws and a set of branchial arches. Pectoral and pelvic girdles are present and remains of the associated fins. (From Broili.)

Palaeospondylus.—From a single quarry in Scotland containing shales of Middle Devonian age have come numerous examples of *Palaeospondylus* (Fig. 43), a tiny animal with a long name, which may be considered as the sole member of the order Palaeospondyloidea. In structure it is far removed from any other early fossil types. There is no trace of dermal armor of any sort, but a considerable series of ossified internal structures has been preserved. There are small plates which appear to have been girdles for paired fins; however, little, if any, trace has been seen of the fins themselves. There was a well-developed caudal fin. While the backbone in most early vertebrates appears to have consisted largely of ordinary cartilage and is hence inadequately known, this tiny form had well-preserved ring-shaped centra and neural arches. There was a well-developed braincase with otic capsules at the posterior corners, and in the center a trough for the brain, roofed at the rear; anteriorly, a series of projections stiffened the rostrum in the presumed nasal region. On the under side of the skull is a series of distinct paired elements of varied shapes. These are difficult to interpret but may represent jaws and gill arches modified for some unusual mode of life. The more anterior sets of these structures are presumably upper and lower jaws; back of them, slender bars may represent the hyoid arch in the simple placoderm condition.

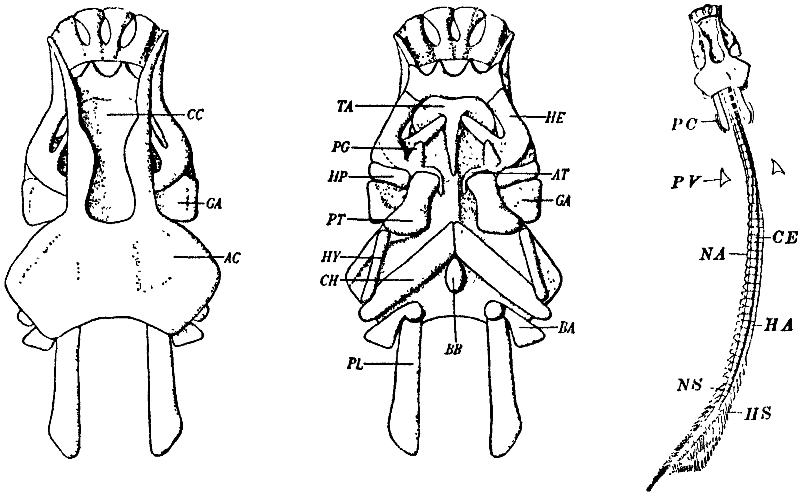


Fig. 43.—*Palaeospondylus*, a small and problematical Middle Devonian fish. *Left*, dorsal view of the skeletal structures of the head region; *center*, ventral view of the same. Dorsally is seen a troughlike cranial cavity (*CC*), roofed posteriorly in the region of the auditory capsule (*AC*). Beneath the braincase are structures difficult to interpret; however *TA* is probably a ventral braincase structure; *HE*, *PG*, *AT*, *HP*, *GA*, and *PT* may be parts of a peculiar jaw apparatus; *HY* is presumably an unspecialized hyomandibular; *CH*, the ceratohyal; *BB*, a basibranchial; *BA* and *PL* more posterior branchial structures. *Right*, the entire fish, the original about 1½ inches long. *PC*, Presumed pectoral girdle; *PV*, pelvic girdle; *NA*, neural arch; *CE*, centrum; *HA*, haemal arch; *NS*, neural spine; *HS*, haemal spine. (After Moy-Thomas.)

The relationships of this little form have been the subject of endless argument. One suggestion is that it was the larval form of some contemporary fish. But usually the vertebrae of small embryos are cartilaginous, and the vertebrae of *Palaeospondylus* are better preserved than those of any of its large contemporaries. It has been considered as an agnathous type, but such features as the presumed limb girdles tend to rule out this conclusion. It is perhaps best to regard it, for the time at least, as a placoderm in which reduction of the armor has reached the end of the story with the complete loss of dermal bone.

The evolutionary position of placoderms.—As reviewed above, the placoderms are a heterogeneous collection of archaic fishes, widely varied in appearance and structure. They possess, however, a number of common features of importance—the presence of bone in the internal skeleton and usually externally as well; the general presence of paired limbs, pectoral and pelvic; and the evidence still further points to the presence generally of a jaw apparatus of a relatively primitive type.

Most of the major groups of placoderms appear at the beginning of the Devonian. We know little of their antecedents, nothing of any Silurian type which could have been a common ancestor. But from a general consideration of placoderms we can perhaps gain some vague idea of what this ancestor must have been like. Presumably there would have been a considerable degree of ossification, both internally and externally. The posterior part of the body was probably scale-covered, the anterior part armored. The presence of a series of bony shoulder plates separate from the head in almost all known placoderms suggests that a similar bipartite arrangement of the armor was present in the ancestral forms. Within the cranial armor, primitive jaws would have been in process of development; along the body, paired and median spines might have been present as an initial stage in fin development. No archaic Silurian fish of this sort has as yet been discovered, but many of the features to be expected in this hypothetical ancestor are found among the known ostracoderm groups.

It is reasonable to assume that the ancestors of the higher bony fishes passed through a placoderm stage in their development, but it is not clear that any of the known placoderm orders represent these ancestors. The sharklike fishes did not appear until relatively late in the Devonian, and it is not impossible that their ancestry might be found to lie among the stegoselachians, were that group better known. Although there are some suggestive resemblances between acanthodians and ray-finned bony fishes, we cannot derive the Osteichthyes from Devonian placoderms, for the first of the higher bony fishes appeared near the beginning of the period. The presence of an operculum combined with the absence of a separate spiracular opening is a stumbling block to the theory that higher fishes originated from placoderms. But this is not an absolute obstacle. The operculum may not have been highly developed in Silurian placoderms; and, in sharks, spiracular specialization may have occurred subsequent to the loss of a gill covering.

CHAPTER 4

SHARKLIKE FISHES

WITH the sharks and their relatives we reach the evolutionary level of modern types of jawed fishes—forms in which the jaws are highly developed, with accompanying modifications of the hyoid arch and spiracular gill slit, and in which the fins and general body structures are built on a more familiar and "orthodox" plan. Such higher fishes are, as far back as our knowledge of them goes, readily separable into two well-defined groups, which may have developed independently, in parallel fashion, from placoderm ancestors. These groups are the class Chondrichthyes, treated in the present chapter, and the Osteichthyes, the higher bony fishes.

Shark characters.—The Chondrichthyes, the cartilaginous jawed fishes, include the sharks and their close allies, the skates and rays, forming the subclass Elasmobranchii, and, in addition, the subclass Holocephali, represented in modern seas by the peculiar chimaeras. As far as their recent representatives are concerned, at least, there are numerous common anatomical characters which readily distinguish them from the Osteichthyes. One obvious feature is that in modern sharks and chimaeras the males bear on their pelvic fins projecting claspers which aid in the internal fertilization appropriate to the large-yolked, shell-covered eggs characteristic of the group. Lungs are absent—a feature presumably associated with a contrast in the environmental history of the two higher fish groups. A majority of modern bony fishes are marine types, but it is generally agreed that they entered the seas at a relatively late date and that their early, lung-bearing ancestors were fresh-water forms. It is quite otherwise with the Chondrichthyes. Apart from one rather aberrant Paleozoic family and occasional later "strays," the cartilaginous fishes appear to have been ocean dwellers since the beginning of their known history. The general story of fish evolution suggests that their ancestors dwelt in inland waters; but the advent of sharklike fishes into the sea was certainly early and was accompanied by special structural and functional adaptations to a saline environment quite different from those evolved (presumably at a later date) by marine bony fishes.

Skeleton.—Most distinctive of the class, however, is the feature implied in the name of "cartilaginous fishes"—the nature of the skeleton. We have seen a great development of bone among ostracoderms and placoderms and will find bone the dominant skeletal element in adult animals among the vertebrates considered in later chapters. In the Chondrichthyes bone is utterly absent. The internal skeleton is purely cartilaginous. These cartilages are, in many cases, calcified, but they never show true bone structure. The dermal skeleton is likewise strongly reduced. Dermal denticles, corresponding to the superficial ornaments of bony plates, may be present; teeth may be abundant and varied; spines of one sort or another are not uncommon; but never are there dermal bones or bony tissues of any sort.

It will be noted that this condition of the skeleton renders the study of chondrichthyan history a difficult matter. Throughout the geological range of the group, finds of isolated teeth and spines are not uncommon; but unless these are similar to types found in modern forms, it is difficult, sometimes impossible, to deduce the nature of the animal which bore them. Calcified braincases or vertebrae are found, but found all too infrequently; ordinary cartilage disintegrates too rapidly to be readily preserved. It is, thus, only under exceptionally favorable conditions that we can gain any idea of the general organization of extinct types of sharklike fishes, and there are many dubious points in the history of the group.

In past times it was generally assumed that the absence of bone in the Chondrichthyes was a primitive condition and that the sharks represented an evolutionary stage antecedent to that of the bony fishes. This assumption appears, at the present day, to be a highly improbable one. Bone, as we have seen, appears in groups much lower down the evolutionary scale; and if we believe the sharks to be primitive in this regard, we must believe, rather improbably, that bone was evolved a number of times by the vertebrates. Nor are the sharks, as one might expect on this assumption, an early group geologically. They are, in fact, the last of major fish groups to appear in the fossil record. No member of the class is definitely known before the middle of the Devonian; even Osteichthyes are present in Lower Devonian strata. It might be argued that absence of an earlier record is due to the fact that the ancestral sharks were soft-bodied and not preserved. But the first sharks were far advanced in the evolution of jaws; and it is difficult to believe that the teeth of these supposed earlier forms should have escaped our attention.

The record, in fact, fits in better with the opposite assumption: that the sharks are degenerate rather than primitive in their skeletal characters; that their evolution has paralleled that of various other fish types in a trend toward bone reduction; and that their ancestry is to be sought among primitive bony, jaw-bearing fishes of the general placoderm type. No well-known placoderms can be identified as the actual ancestors of the Chondrichthyes. An approach to such an ancestral type is seen in the acanthodians, however, and we have noted that some of the peculiar stegoselachians appear to show morphologically intermediate stages in skeletal reduction. Increasing knowledge of Lower Devonian placoderms may some day bridge the gap.

Primitive elasmobranchs.—The Chondrichthyes, living and fossil, appear clearly separable into two subclasses, the Elasmobranchii and the Holocephali. Of the two, the elasmobranchs—the sharks and related types – are not only the better known but appear also to be more primitive in nature and therefore merit first consideration.

The oldest geological record of the sharks is in American Middle Devonian beds, in which are found a few specimens of the type of tooth known as *Cladodus* (Fig. 44), a type characteristic of various early elasmobranchs. These teeth are found in considerable numbers in Carboniferous rocks and finally disappear in the early Permian. They consist of a tall central cusp with a broad base on which are found one or more pairs of smaller lateral tubercles.

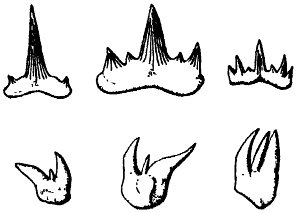


FIG. 44

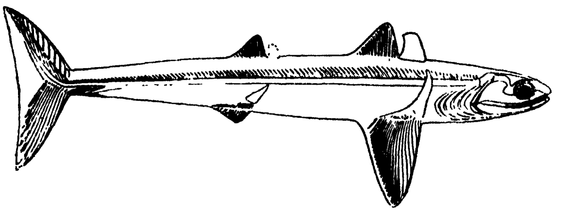


FIG. 45

FIG. 44.—*Above, Cladodus* teeth from the late Devonian and Carboniferous; *below*, pleuracanth teeth from the Permian. Somewhat reduced.

FIG. 45.—*Cladoselache*, a late Devonian sharklike fish. Original specimens range from about 1½ to 4 feet in length. In addition to the normal paired fins, a pair of horizontal "rudders" may be noted at the base of the tail fin. Some specimens, at least, had a spine in front of the first dorsal fin; whether one was present on the second dorsal is uncertain. (From Harris, partly after Dean.)

In the Cleveland shales of the late Devonian an exceptional type of preservation has given us numerous specimens of *Cladoselache*, a shark possessing this tooth type, in which much of the body structure can be made out (Figs. 45, 46). This form is found in nodules in which are preserved not only the remains of the teeth and calcified cartilages of the skeleton but also impressions of the skin and body outline, and even traces of such soft tissues as muscle and kidney. There were two dorsal fins, each with basals and radials consisting of parallel rods of cartilage. These fins have usually been thought to be spineless, but it has recently been discovered that dorsal-fin spines were present in at least some individuals. The tail fin was very markedly heterocercal, the posterior end of the vertebral column tipping sharply upward. Well-developed pectoral and pelvic fins were present, the former much the larger, while far back at the base of the tail fin and just in front of the supposed position of the anus was a pair of outgrowths from the side of the body, seemingly a third pair of fins, absent in later sharks. Like the median fins, the pectorals (Fig. 26, *A*) and pelvics had a skeleton in which the projecting portion—the radials—consisted of long, unjointed, parallel rods of cartilage. The basal portion of the fin is elongated anteroposteriorly, sometimes consisting of discrete blocks of cartilage forming an axis within the body wall, sometimes consisting of a single fused basal structure. The fin was a very broad-based flap, with limited possibilities of motion. It is quite probable, as we have previously noted, that this is a very primitive type of fin structure from which may have arisen, by a constriction of the base, the fan-shaped fin of most later sharks and even the leaf-shaped appendage of a number of Paleozoic fish types. We have seen that in those placoderms in which the fins are known, the parallel-bar structure is common. There, however, the fin is typically developed behind a prominent spine. In *Cladoselache* the paired fins are spineless; but it is possible that the spineless condition is a secondary one. It may be emphasized that no trace has been found in *Cladoselache* of the claspers which are characteristic of later shark types.

The braincase and jaws are fairly well known; they were very similar to those seen in *Pleuracanthus* and illustrated in Figure 55. The jaws were amphistylic. They were supported, in part, by a moderately developed hyomandibular. In addition, the upper jaws articulated with a prominent postorbital process, and there was apparently an additional articulation with the base of the braincase farther forward. This type of jaw suspension is apparently the primitive one for elasmobranchs but is very uncommon in modern sharks. There were large paired eyes, with concentric rows of denticles about them, and paired nostrils. Behind the jaws (Fig. 46) lay the hyoid and five succeeding branchial arches.

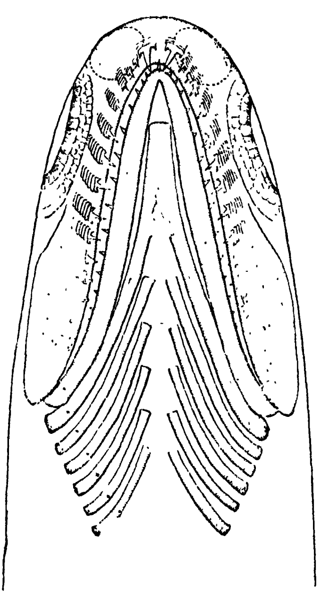


FIG. 46.—Ventral view of head and throat region of *Cladoselache* to show the ventral segments of the branchial arches and the jaws seemingly homologous with them. The position of the nasal capsules is indicated by dotted outlines; the orbits, seen laterally, are surrounded by enlarged scale-like denticles. (After Dean.)

The essential features of *Cladoselache* are repeated in another sharklike fish of equal antiquity—*Ctenacanthus*, present from Upper Devonian to Lower Permian; its characteristic fin spines are found abundantly in the Carboniferous. In *Ctenacanthus* very stout spines, with numerous beaded, longitudinal ridges, acted as cutwaters for the dorsal fins. The dentition—of

Cladodus teeth—was identical with that of *Cladoselache;* the paired fins were of similar structure, except that the radial elements were segmented, as in modern sharks, rather than single rods. It is probable, however, that there was a normal anal fin rather than the peculiar paired structures reported here in *Cladoselache.*

Cladoselache and *Ctenacanthus* may be considered as representative of a very primitive order of sharklike fishes, the Cladoselachii. The amphistylic jaw suspension, the broad-based fins, and the absence of claspers are diagnostic and primitive characters. It is not improbable that the cladoselachians are close to the base of the entire chondrichthyan assemblage.

Hybodonts.—The ancient cladoselachians became extinct during the Permian; they were replaced by more progressive sharks, presumably descended from them, which appear to have come into existence at the end of the Devonian and flourished in the late Paleozoic and the Mesozoic. These sharks—the hybodonts—form an intermediate stage in selachian evolution.

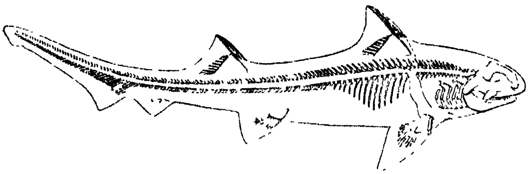


FIG. 47.—*Hybodus hauffianus,* a Mesozoic shark; original about 7½ feet long. (From Smith Woodward.)

They differ from the typical modern forms in that the amphistylic type of jaw support is retained; they had, however, advanced considerably as regards their paired fins. The latter were, as in living sharks, flexible, narrow-based structures rather than rudder-folds. Seemingly, this more flexible type of fin had evolved from that of cladoselachians by the freeing of the posterior margin from the body wall so that the basal elements project outward into the fin itself. These basal elements in the pectoral fin usually consist, in both hybodonts and modern shark types, of three elements—propterygium, mesopterygium, and metapterygium, the last the most important of the three; the pelvic fin is similarly built but usually simpler in structure. An important feature is the fact that claspers (Fig. 24, *D*) had developed on the pelvic fins of the males. These structures are present in all the sharks yet to be considered (as well as the skates and rays derived from them), and cause us to separate all these forms as an order, Selachii, from the archaic cladoselachians.

Best-known of primitive selachians is *Hybodus*, a common Mesozoic shark (Figs. 6, 24, 47). The general appearance is, for the most part, quite similar to that of cladoselachians, and a striking resemblance to *Ctenacanthus* lies in the fact that the dorsal fins and their spines are almost identical in nature (the striated spines can be distinguished, however, by the smooth rather than beaded ridges). The braincase is somewhat shortened, after the fashion of modern sharks; the jaws are, however, still typically amphistylic.

The dentition shows some variation in the hybodont group but tends to adhere to a single general pattern. The teeth are readily derivable from those of the *Cladodus* type. Those near the front of the mouth are generally sharp-cusped. Farther back in the jaws, however, the cusps are usually lower, often blunt, and sometimes completely reduced, so that a low, rounded crown is produced. In all sharks replacement teeth are formed in rows inside the jaw and gradually swing up into place (Fig. 48). In hybodonts it appears probable that a number of replacement teeth in each row were exposed and functioning at the same time. This feature, together with the flattening of the back teeth, results in the development posteriorly of broad triturating surfaces, suitable for crushing mollusks; the numerous sharp anterior teeth were used for seizing prey. A wide variety of food was thus available to the hybodonts.

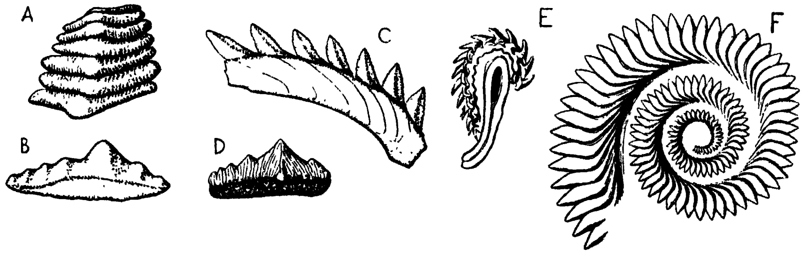


FIG. 48.—The teeth of primitive selachians. *A*, *Orodus* (Carboniferous), crown view of a tooth series (×¾); *B*, same, lateral view; *C*, *Edestus* (Carboniferous) tooth whorl, reduced; *D*, *Hybodus* (Triassic) natural size; *E*, section through the jaw of a Recent shark to show a crowded row of replacement teeth; *F*, a tooth whorl, presumably placed in the jaw symphysis of the Permian *Helicoprion* (reduced)—the earlier teeth were not shed as in typical sharks but were apparently retained and buried in the inner part of a complex spiral of replacing teeth. (*C* after Dean; *E*, *F* from Smith Woodward.)

Hybodus is a Mesozoic form; a number of sharks of this sort were present during that era and were especially common in the Jurassic. They were, however, a much older group. There are a few teeth which may be hybodont in nature in the Upper Devonian, suggesting that at an early date the hybodonts had evolved, through tooth and fin modifications, from the primitive cladoselachians. In the Carboniferous, teeth and spines of *Orodus* and other genera are not uncommon finds.

In many hybodonts (as in such older fishes as acanthodians) there appears to have been a central series of teeth in the mid-line of both upper and lower jaws; and in some late Paleozoic genera, as *Edestus* and *Helicoprion* (Fig. 48), these symphysial whorls may be highly developed. In *Helicoprion* the teeth, in contrast to usual shark conditions, did not drop out after they had reached the edge of the jaw but curved downward and inward to form the core of a complex growing spiral. In some of these forms the microscopic structure of the teeth resembles that of the Holocephali, discussed later, and it may be that this group of peculiar fishes has originated from the hybodont group.

In the Carboniferous seas, cartilaginous fishes were abundant—predaceous cladoselachians and a wide variety of mollusk-eating holocephalians, as well as the omnivorous hybodont sharks. Most of these types disappeared before the end of the Paleozoic. This may be correlated with a marked change at this time in the nature of the marine invertebrates, a change to which these sharks, directly or indirectly dependent upon them for food, failed to adapt themselves. Only the seemingly versatile and omnivorous hybodonts survived into the Triassic. During the Mesozoic many sharklike fishes became once more adapted to invertebrate diets, and numerous bony fishes entered the sea to form an additional source of food supply. There began, from the hybodonts as a basal stock, a great deployment of more modern types of sharks and of the related skates and rays.

Primitive shark survivors.—The hybodonts themselves have been extinct since the Cretaceous. There are, however, archaic sharks which appear to be relatively primitive descendants of the old *Hybodus* group.

The Port Jackson shark, *Heterodontus* [*Cestracion*] of the Pacific Ocean is in many respects a little-modified hybodont descendant. Like those ancient forms, this shark is, in great measure, a mollusk-eater and retains the hybodont type of dentition, with sharp anterior fangs and low, rounded posterior teeth, forming a shell-crushing apparatus. Its general appearance and structure, including the presence of stout spines on its two dorsal fins, is comparable to that of hybodonts. In its jaws, however, there has been a structural change, for the palatoquadrate no longer articulates, as did that of the older sharks, with a postorbital process of the braincase. Nevertheless, *Heterodontus* is still fundamentally amphistylic, for the the upper jaws are firmly braced against the braincase more anteriorly and ventrally, as well as receiving support from the hyomandibular. Several genera of the later Mesozoic appear to be intermediate between the hybodonts and this group, and *Heterodontus* itself appeared in the Jurassic.

Other archaic surviving families are those represented by *Hexanchus* [*Notidanus*] and *Chlamydoselache*. These are slender-bodied, fast-swimming predaceous sharks, lacking fin spines and having but a single dorsal fin—features in which they are quite different from the hybodonts. Six or seven gill slits, rather than five, are present, possibly a primitive feature but equally possibly a secondary increase. All the teeth (Fig. 49) are sharp-cusped but quite unlike those of the older protoselachians; in *Hexanchus* they are peculiar saw-toothed structures; in *Chlamydoselache*, three-pronged and superficially comparable to those of pleuracanth sharks of the Paleozoic. In their jaw structure, however, they are persistently primitive. *Hexanchus* has the postorbital connection of upper jaw and braincase developed as in the oldest sharks; in *Chlamydoselache* the jaw fails (barely) to make contact here, but the construction is still essentially amphistylic. Both sharks are rare today. *Chlamydoselache* is represented as a fossil by only a few teeth from the Tertiary; *Hexanchus*, however, had developed in the Jurassic.

"Modern" sharks.—In the more typical modern sharks remaining for consideration, direct articulation of jaws with braincase has been abandoned, and the jaws are hyostylic, supported solely by a prop formed by the large hyomandibular. Selachian development in this "modernized" phase began in the Jurassic; and a rapid deployment resulted, before the close of the Mesozoic, in the appearance of most of the dozen or more existing families. Two main lines of development were early evident, and most of these sharks can be readily grouped into two suborders, the Galeoidea and the Squaloidea.

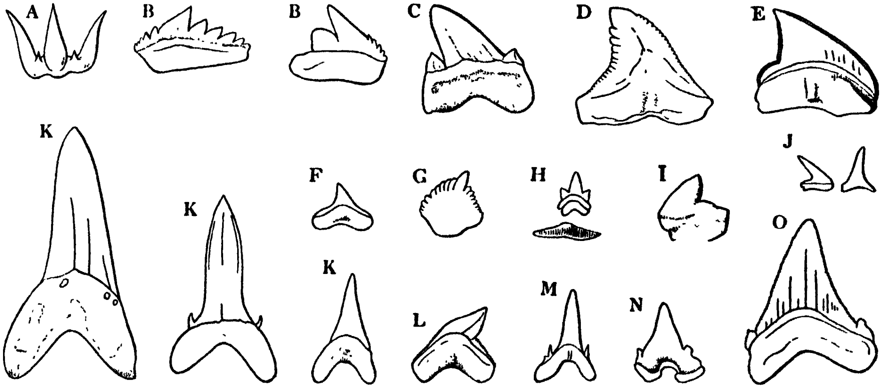


Fig. 49.—Teeth of various Cretaceous and Tertiary sharks: *A*, *Chlamydoselache; B*, *Hexanchus; C*, *Otodus; D*, *Hemipristis; E*, *Squalicorax* [*Corax*]; *F*, *Sphyrna; G. Ginglymostoma; H*, *Heterodontus*, anterior and posterior teeth; *I*, *Squalus; J*, *Rhina* [*Squatina*]; *K*, *Isurus; L. Galeocerdo; M*, *Scapanorhynchus; N*, *Scylliorhinus* [*Scyllium*]; *O*, *Carcharodon*. Mostly half natural size; *Rhina*, and *Squalus* somewhat enlarged; *Carcharodon* ×¼. (After Fowler and Smith Woodward.)

The galeoids, including the great majority of the living sharks, are, in general, active predaceous types, with fusiform bodies which are not at all depressed, the spiracle small or even absent, and an anal fin always present. The oldest forms are from the Upper Jurassic, when there appear two genera related to modern small sharks. One, *Galeus* [*Pristiurus*] is a living genus of dogfishes ("topes"); the other, *Palaeoscyllium*, is closely related to the former and to *Scylliorhinus* [*Scyllium*], the common spotted dogfish of European waters, which appears in the Cretaceous.

In this latter period galeoid sharks have diversified into a number of genera, most of them abundantly represented by teeth in Tertiary marine deposits and surviving to the present day (Fig. 49). We may cite some common forms *seriatim: Carcharias* [*Odontaspis*], the sand sharks, with large, awl-shaped teeth; *Scapanorhynchus*, the long-snouted "ghost shark"; *Isurus* [*Lamna, Oxyrhina*], the mackerel or porbeagle sharks, with long, slender, flattened teeth; *Carcharodon*, the large white shark—a maneater—bearing large triangular teeth with serrate edges (one Tertiary species may have had a mouth gape of 6 or 7 feet); *Squalicorax* [*Corax*] of the Cretaceous and early Tertiary, with hook-shaped serrate teeth; the nurse shark, *Ginglymostoma; Galeocerdo*, the tiger shark; *Hemipristis*, common in the early Tertiary; *Sphyrna* [*Zygaena*], the hammerhead, with eyes placed on peculiar lateral projections of the head. Still other common types appear in the early Tertiary, including *Alopiopsis*, the long-tailed thresher shark; *Mustelus*, the smooth dogfish or "hound"; and *Galeolamna* and related genera of common sharks (frequently but incorrectly called *Carcharinus*).

A further series of sharks not uncommon at the present day is that of the Squaloidea. This group shows certain features suggestive of an approach toward bottom-dwelling habits and the condition seen in the skates and rays. As in them, the spiracle is usually large, and the anal fin is lacking; the body, however, is well rounded in squaloids, and the pectoral fins are of normal shape. This group of sharks is as old a one as the galeoids. *Protospinax*, a form related to the modern spiny dogfish (*Squalus*) is an Upper Jurassic shark, and in the Cretaceous there appear a number of representatives of this group.

To be considered as sharks rather than as skates or rays are two additional forms—the saw shark *Pristiophorus*, and *Rhina* [*Squatina*] (Fig. 52, *A*). The former has a long-toothed rostrum, like the saw rays noticed below, and a flattened head, but is otherwise similar to the squaloids. Saw sharks are known from the Upper Cretaceous. *Rhina*, the angel shark, is still more ancient, appearing in the Jurassic, and seems to point definitely toward the skate type of organization; for the body is flat, the eyes are dorsal in position, and the pectoral fins are much enlarged. However, the gills are lateral in position rather than ventral (as in skates), and the pectorals lack any attachment to the head, so that we must consider *Rhina* as a shark, although a very skatelike one.

Skates and rays.—All remaining elasmobranchs may be included in an order which we may term the Batoidea, in contrast with the order Selachii, the true sharks just discussed. They comprise a series of forms which have become bottom-living types, often very depressed in shape. The eyes are dorsally placed; the spiracle, used for intake of water, is much enlarged; the gills are ventral in position; and the anal fin is lost, as in squaloid sharks, in correlation with bottom-dwelling. The enormously expanded pectoral fins extend forward above the gills to attach to the sides of the head. Swimming is accomplished by an up-and-down motion of these large fins; the tail tends to be reduced and is often a mere whiplash; the dorsal fins are reduced or absent. Skates and rays are mostly mollusk-eaters, and in correlation with this the teeth (Fig. 53) are usually flattened and often form a solid crushing pavement.

Within this group many varied types have been developed. The most primitive members, and among the oldest in their geological appearance, are types intermediate in structure between sharks and rays —forms in which the pectoral fins are enlarged but in which the body is still somewhat rounded and well-developed dorsal and caudal fins are still present. *Rhinobatis* (Fig. 50), the living banjo fish, is a form of this sort which was already in existence in the Jurassic. Sawfishes (Fig. 51) were common in the Upper Cretaceous, and *Pristis* is a surviving genus of this group. They resemble the banjo fishes in their general organization but are notable for the development of a long rostrum armed with teeth on either margin. We have mentioned a similar development in *Pristiophorus;* but in that saw shark the diagnostic skate characters are absent, and the two groups are generally regarded as exhibiting parallel development rather than any close relationship.

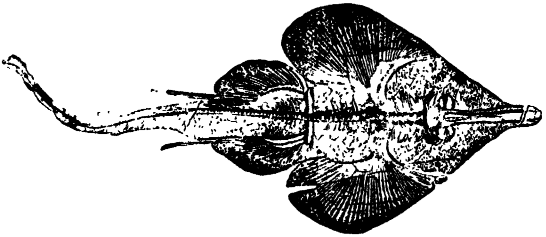


FIG. 50.—*Rhinobatis*, the "banjo fish," a primitive skate; about $\frac{1}{20}$ natural size. (From Smith Woodward.)

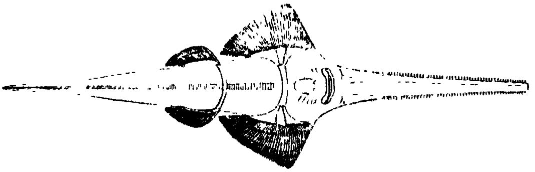


FIG. 51.—*Sclerorhynchus*, a Cretaceous sawfish; about 3 feet in length. (From Smith Woodward, *Outlines of Vertebrate Paleontology*.)

In the Cretaceous, typical skates and rays, including most of the modern types, were present. In *Raja* (Fig. 52, *B*), still a common skate today, we find developed the normal characters of the group, such as a short body, very broad pectoral fins extending forward along the sides of the snout, a slender tail, and median fins reduced almost to the vanishing-point. In the Cretaceous were also present the sting rays of the *Trygon* type (Fig. 52, *C*), commonly with a poisonous "stinger" developed from a modified fin ray on the tail; the pectoral fins are so expanded laterally that the body is broader than long and so greatly produced anteriorly that they are fused in front of the snout. Still another group to develop at that time was that of the eagle rays, such as *Myliobatis* (Fig. 52, *D*) and *Rhinoptera*. Here the fins are greatly expanded laterally but do not meet in front of the head, and the mouth has a highly developed pavement of flat crushing teeth (Fig. 53). *Ptychodus* (Fig. 53) is representative of a family of Cretaceous skates known only from their rounded and sculptured teeth. In the Tertiary, skates and rays are known from numerous localities, and a final addition to the roster of fossil skates is made by the appearance in the Eocene of the torpedoes (Torpedinidae), with rounded bodies in which some of the musculature is modified into powerful electric organs.

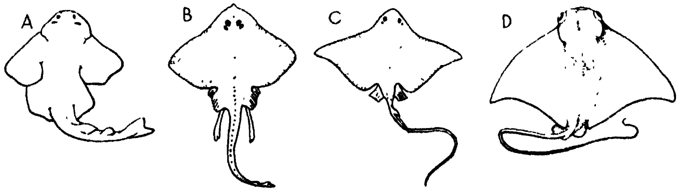


FIG. 52.—Various skates and rays: *A*, *Rhina* [*Squatina*]; *B*, *Raja*; *C*, *Trygon*; *D*, *Myliobatis*. These forms are known both from living representatives and from Tertiary fossil types. (*A–C* after Goodrich; *D* after Bridge.)

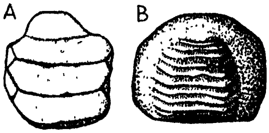


FIG. 53.—Teeth of rays. *A*, Part of a fossil dental battery of *Myliobatis*, with three complete plates and fragments of others. *B*, a single tooth of the large Cretaceous skate, *Ptychodus*. One-half natural size.

Pleuracanths.—An early side branch from the "main line" of elasmobranch evolution is that seen in the order Pleuracanthodii. These, in contrast to most shark types, were fresh-water forms. They appeared in the late Devonian, and were abundant in the Carboniferous and early Permian; a few persisted into the Triassic. The body of *Pleuracanthus* (Figs. 54, 55) was long and slim, with an elongated dorsal fin stretching far down the back. The tail, unlike that of most early fishes, was diphycercal; but the tip tilted slightly upward, suggesting derivation from a heterocercal ancestor. The anal fin was a peculiar double structure. The paired fins (Fig. 24, *C*, *D*) were of the archipterygial type, with a main axis and side branches. This type of fin may have been derived by the gradual development of a posterior axis from one of cladoselachian type; the branches were not fully developed on the posterior margin of the axis, suggesting a transitional condition. A clasper is present in the males.

There were no dermal plates on the skull; the braincase, jaws, and branchial arches are sometimes preserved in calcified cartilage; the jaw construction is of the typical amphistylic type seen in *Cladoselache*. A long movable spine, bordered by two rows of small denticles, projected from the back of the head. The teeth, loosely attached to the jaws, typically consisted of two divergent prongs and a central cusp (usually small), set on a button-like base (Fig. 44).

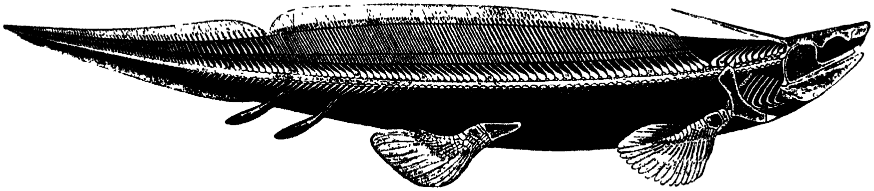


FIG. 54.—*Pleuracanthus*, a Carboniferous and Permian sharklike form; an average specimen perhaps 2½ feet long. (After Fritsch, from Smith Woodward.)

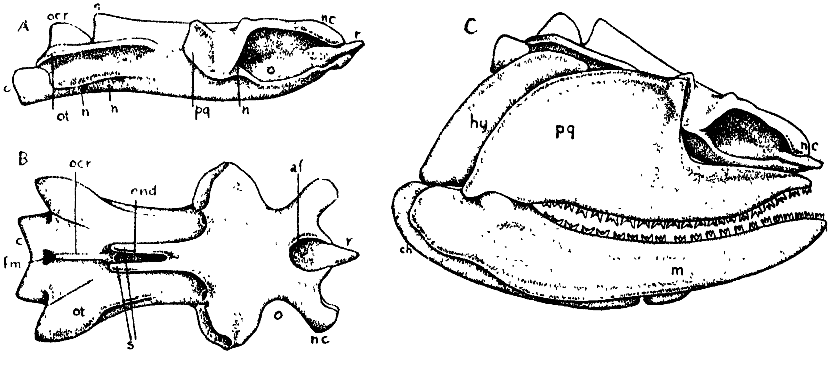


FIG. 55.—The cranial anatomy of a Paleozoic "shark," *Pleuracanthus*. *A*, Latera lview of braincase, *B*, dorsal view; *C*, lateral view with jaw and hyoid arch articulated. One-third the size of a large specimen. Abbreviations: *af*, anterior opening (fontanelle) in roof of braincase; *c*, occipital condyle; *ch*, ceratohyal; *end*, common opening for endolymphatic ducts from internal ear; *fm*, foramen magnum; *hy*, hyomandibular; *m*, mandible; *n*, exits for certain cranial nerves; *nc*, nasal capsule; *o*, orbit; *ocr*, occipital crest for attachment of body muscles; *ot*, otic region; *pq*, upper jaw (palatoquadrate bar) and its point of attachment to postorbital process of braincase; *r*, rostrum; *s*, paired processes to which a large spine (peculiar to pleuracanths) is attached.

Little is known of the ancestry of the pleuracanths. In some cases teeth are known in which the three cusps are nearly equal in size, suggesting a derivation from the *Cladodus* type by a reduction of the central cusp and emphasis on the lateral ones. The presence of claspers suggests a fairly close relationship to the modern sharks and the chimaeras.

Chimaeras.—Among the cartilaginous fishes of modern times we find, besides the sharks and skates, a second group, relatively rare and quite different in many features. These are the chimaeras or ratfish. They are fairly actively swimming types but often with the tail fin reduced to a whiplash, with little indication of its true heterocercal nature. In many features (such as the construction of the paired fins and the presence of a clasper) they resemble the elasmobranchs. But there are some striking differences (Fig. 56). There is often a large rostrum, and the males have an odd clasping organ on the "forehead." Dermal denticles are absent from the skin; there is a large spine in front of the dorsal fin; and the pectorals are enlarged and fan-shaped. The gills are covered with a flap of skin, an operculum, contrasting with the open slits of the sharks; and there is no spiracle. The usual dentition consists merely of a large toothplate on each jaw ramus and an additional pair of plates at the front of the upper jaw. This construction appears to be related to the mollusk-eating habits of chimaeras. The upper jaws are firmly united with the braincase, giving a firmer leverage for the bite; this unusual fused condition gives its name to the subclass and is probably secondary. There is, of course, no need of support for the jaws from the hyomandibular, and the hyoid arch is attached to neither jaws nor braincase.

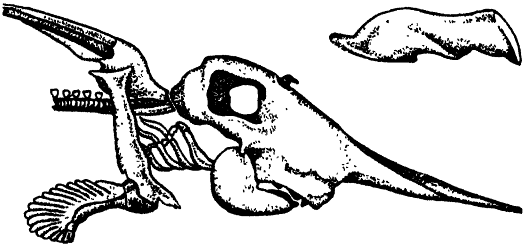


FIG. 56.—Skull and shoulder region of a Jurassic chimaera, *Acanthorhina*. (After Fraas.) About ⅓ natural size. *Upper right*, mandibular dental plate of the Jurassic chimaera, *Myriacanthus*. (After Dean.)

These deep-sea fishes are far from common today, but occasional toothplates and spines are found in Tertiary and Cretaceous deposits; there are further remains in the Jurassic and possibly in the Triassic. Until recently we have had little idea as to their earlier ancestry. It is not impossible that they have evolved independently from placoderm ancestors; however, the presence of such typical elasmobranch features as the claspers suggests that they represent a group derived from early elasmobranchs, but different enough to merit the erection for them of a separate subclass, to which the term Holocephali may be applied.

Bradyodonts.—The ancestors of the chimaeras are apparently to be sought among a series of poorly known Paleozoic cartilaginous fishes grouped as the order Bradyodonti. These were eaters of mollusks or other hard invertebrates, for the teeth are arranged as crushing plates. The group name refers to the fact that tooth replacement, in contrast to that of sharks, was a slow process, and the dental plates appear to have been more or less permanent structures. The bradyodonts appeared at the end of the Devonian and were very abundant during the Carboniferous but disappeared before the opening of the Mesozoic. They are known, for the most part, only from their teeth, although there are numerous Carboniferous fin spines which may belong to bradyodont genera. Four families are generally distinguished; it must be noted that there is no proof that they were at all closely related to one another, and the group is quite possibly an artificial one.

1. *Cochliodonts.*—This family is phylogenetically the most important of the bradyodonts, for it appears to show a transition between primitive sharks, on the one hand, and chimaeras, on the other. In typical genera, such as *Cochliodus* and *Deltodus* (Fig. 57, *C*) the main tooth structure consists of a long spirally curved plate in each half of each jaw, although there appear to have been smaller anterior teeth. These toothplates are quite comparable to those of Jurassic chimaeras. The toothplates are usually solid, unified structures, but there were often cross-lines which suggest that they had arisen through the fusion of a series of teeth. In *Helodus* (Fig. 57, *B*) separate teeth were still present; these appear to be readily derivable by a process of flattening from the *Cladodus* type of early elasmobranchs (cf. *Orodus*, Fig. 48, *A*). In two instances the entire fish has been preserved. In *Helodus* (Fig. 58), as in chimaeras, the pectoral fins were large; the body in cochliodonts was rather flattened, in a fashion somewhat parallel to that of the skates (of similar habit); and, significantly, the upper jaw was, as in chimaeras, solidly fused with the braincase.

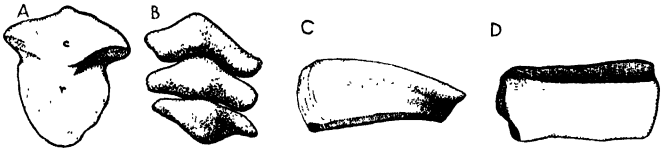


Fig. 57.—Teeth of bradyodonts. *A*, *Petalodus* ($\times\frac{1}{2}$); *c*, crown; *r*, root. *B*, *Helodus*, three teeth, crown view ($\times\frac{3}{2}$). *C*, *Deltodus*, crown view ($\times\frac{1}{4}$). *D*, *Psammodus* ($\times\frac{1}{2}$).

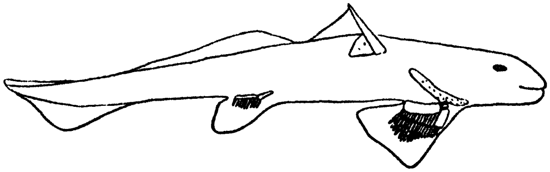


Fig. 58.—*Helodus*, a Carboniferous bradyodont, length about 14 inches. (From Moy-Thomas)

2. *Petalodonts* (*Petalodus* [Fig. 57, *A*]).—The teeth of these forms have broad, lozenge-shaped crowns, which appear to have been applied closely to those adjacent, a group of such teeth forming a solid crushing pavement. Each tooth had a long root, sometimes subdivided, extending downward at an angle from the surface of the crown. In two cases there are indications of body contours. These fishes are much more raylike than the cochliodonts, with a much depressed build and greatly enlarged pectoral fins.

3. *Psammodonts.*—In this family and the following, the toothplates only are known. In *Psammodus* (Fig. 57, *D*) the dentition consisted of a few large quadrilateral plates arranged above and below in two rows which met in the mid-line. The origin of these plates is obscure; and while they were probably formed by a fusion of teeth, there is no indication of this in the specimens.

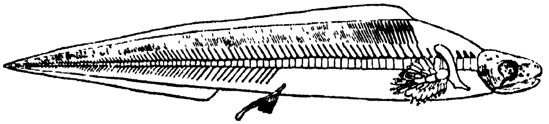


FIG. 59.—*Chondrenchelys*, a small Carboniferous fish allied to the bradyodonts but with a body resembling that of pleuracanth sharks; length of original, 7 inches. (After Moy-Thomas.)

4. *Copodonts.*—The dentition in this rare and obscure group consisted of a single subquadrate tooth medially placed at the front end of the upper and lower jaws.

With the bradyodonts may be provisionally grouped *Chondrenchelys* (Fig. 59), a small cartilaginous fish from the Mississippian of Scotland. As in other holocephalans, the upper jaws were fused with the skull, and the mouth was armed with a series of plates comparable, in general, to those of cochliodonts. The postcranial skeleton, however, was of a very different nature. There were no fin spines of any sort; but in other respects the body was very similar to that of the pleuracanths, for the tail was of the diphycercal type, there was a long dorsal fin continuous with the caudal, and the paired fins were of the archipterygial type. Presumably, however, these pleuracanth resemblances are due to parallelism rather than to real relationship.

CHAPTER 5

BONY FISHES

THE groups thus far considered, although prominent in the older geologic periods, have in later times become much reduced in numbers; the higher bony fish constituting the class Osteichthyes have, on the other hand, continually increased in importance. Appearing in the Middle Devonian fresh waters, they flourished greatly and by the end of the Paleozoic had almost sole possession of the lakes and streams. By that time they also had invaded the seas, and at the present time the group includes not only all fresh-water fishes but also the vast majority of marine forms as well.

As discussed here, the bony fishes will be grouped in two subclasses—Actinopterygii and Choanichthyes—already quite distinct at their first appearance in the fossil record. The former were, at first, rare but rapidly became the dominant types; their modern representatives, the teleosts, are the common fishes of today. The Choanichthyes, or fishes with internal nostrils (choanae), include the Crossopterygii, ancestral to land vertebrates, and the aberrant Dipnoi, the lungfishes. Flourishing at first, these groups are now close to extinction.

The Osteichthyes may be briefly defined as bony fishes with a specialized spiracle and hyoid support for the jaws. Bone is not a new material in the Osteichthyes, but its retention here is a useful point of distinction between these fishes and the Chondrichthyes, which also have a highly developed jaw apparatus but have lost all vestiges of bony structure. The presence of some sort of lung or air sac seems to have been a characteristic of all early Osteichthyes; this feature is in contrast with conditions in other surviving fish types, although, as noted previously, a lung may have developed at a still earlier stage in fish history.

The primitive members of both subclasses appear to have been active swimming types with a fusiform body and a heterocercal caudal fin. This last structure may be variously modified, and in almost all later members of the class the tail tends to become a symmetrical structure. In lungfish and crossopterygians this symmetry is attained by the evolution of a diphycercal tail; in the ray-finned types superficial symmetry was reached by a different process. One dorsal fin was present in the earlier actinopterygians, two in the Choanichthyes; a single anal is found in all.

Skeleton.—Bone appears to have been a common feature in ancestral vertebrates. But in the fish classes already considered, ossification is, in general, far from complete in forms so far discovered, and there was a strong tendency toward bone reduction and the retention of the embryonic cartilaginous state. In early Osteichthyes, on the other hand, skeletal ossification was of an advanced nature; and, while there is even here a trend toward reduction, this trend is, in general, much less marked; the process of bone development is, so to speak, much more firmly imbedded in the embryological pattern of these fishes. A dermal covering of thick scales and plates was present in the most primitive Osteichthyes. These structures may be much modified but are seldom lost. The internal skeleton, too, was highly ossified in early bony fishes, except for a few structures, such as the vertebral centra. In most later members of the class these internal bones are preserved with little loss, and there may even be further progress in ossification of the backbone. In only two groups are there conspicuous regressions from a highly ossified condition: the sturgeons and paddlefishes among the Actinopterygii and the later lungfishes among the choanate forms.

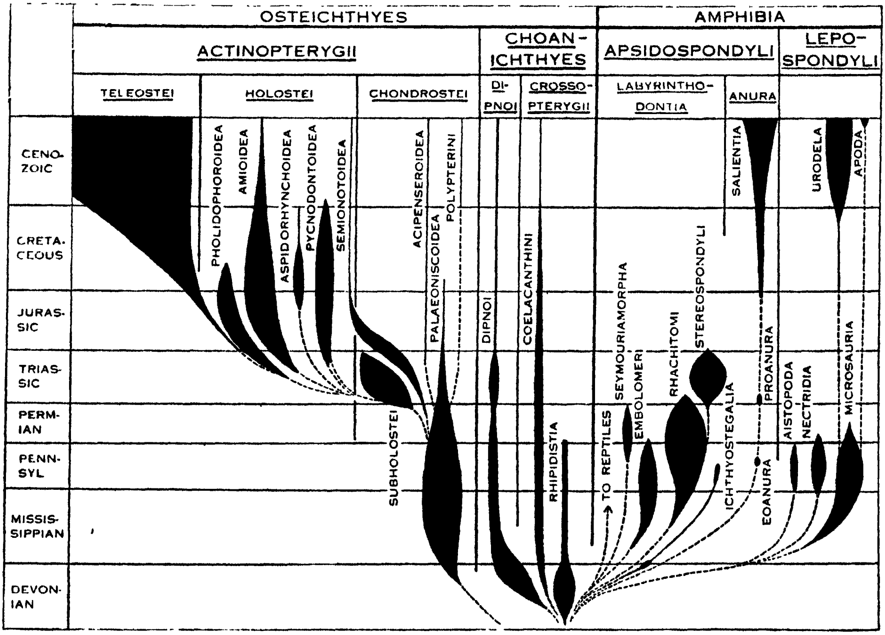


FIG. 60.—Development of the groups of bony fishes and amphibians

Scales.—In the older bony fishes the trunk and tail were completely incased in an armor consisting of continuous and usually overlapping rows of bony scales, presumably rhomboidal in shape in the most primitive stage. Two main types of scale are found in early bony fishes—the cosmoid and the ganoid (Fig. 61). The former type was present in primitive crossopterygians and lungfish. Its base consisted of bone arranged in parallel layers. Above was a layer of spongy bone filled with spaces for blood vessels. The upper part of the scale consisted of a substance termed cosmine, similar to the dentine of teeth, arranged about numerous pulp cavities; the surface was covered with a thin layer of enamel-like material. The whole suggests a series of fused denticles united with a basal plate of dermal bone (or rather, as was suggested, shark denticles represent superficial pieces of such scales which have "floated free" with the dissolution of the underlying bony plate).

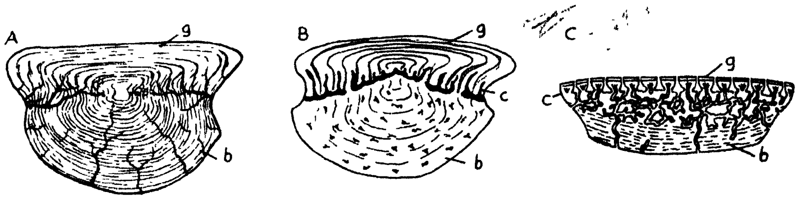


FIG. 61.—Vertical sections through the scales of: *A*, *Acanthodes*, an acanthodian shark; *B*, *Cheirolepis*, a Devonian actinopterygian; *C*, *Megalichthys*, a Carboniferous crossopterygian. All highly magnified; Abbreviations: *b*, basal layers of bone or bonelike material; *c*, cosmine layer; *g*, superficial region—enamel or layers of enamel-like material (ganoine). (After Goodrich.)

A second ancient type, found in the older actinopterygians, was the ganoid scale. The same three units are present as in the cosmoid scale, but here the enamel-like material, deposited in thick layers, is termed ganoine. Embryologically these scales arise by the deposition in onion-like fashion of concentric layers of all three materials around a central core composed of a single "cosmoid-scale" unit. It is of interest that almost the same type of scale was present in acanthodians. Possibly the ganoid scale is the primitive type, and the cosmoid has resulted from a reduction of the superficial ganoid layers; or, conversely, the ganoid type has developed by elaboration from a simple cosmoid structure.

The term "ganoid" is often used to designate certain ancient bony fish. Properly, such a term may be applied to primitive actinopterygians which have scales of the ganoid type. But frequently (and unfortunately) it is applied to any primitive-looking fish with thick shiny scales and to forms with cosmoid, as well as ganoid, scales.

Both types of scale have undergone great modification and reduction; only one living fish has a cosmoid scale; few have the ganoid type. In both subclasses there was a strong tendency toward the loss of both the enamel-like surface and of the underlying cosmine, leaving a relatively thin and simple bony scale.

Skeleton of the head (Figs. 62, 63).—The cranial skeleton is of a double origin, consisting of dermal bony plates comparable to enlarged scales and of internal bones replacing embryonic cartilages; in skull and jaws (and even in the shoulder girdle) these two types of components are combined to form complex structures. Similar complexes were present in ostracoderms and placoderms, but our relative lack of knowledge of internal anatomy in these forms and the frequent lack of ossification have caused our account of them to be brief and inadequate. In the sharks the absence of dermal components has resulted in a deceptive and probably secondary simplicity. In the Osteichthyes, however, there emerges a general pattern of cranial construction, which, although complex, merits description in detail not only because it is to be found in all subdivisions of the group but because it is the basal plan upon which the skulls of all tetrapods are built.

We shall note in preliminary fashion the essential units of which it is constructed before considering in more detail the various dermal and cartilage-replacement bones which take part in its formation. The skull itself is made up of three units: (1) an ossified braincase, comparable to that of a shark, with a dermal bone below it; (2) upper jaw and palatal structures, including ossified equivalents of the cartilaginous shark upper jaw and additional dermal bones of the palate; and (3) a shield of dermal bones covering the top and sides of the head and in contact with the deeper structures already noted (cf. Fig. 8). Additional skeletal features of the anterior part of the body include (4) the lower jaw, also a combination of dermal elements and replacement bones; (5) the gill arches, including a prominent hyomandibular, all endochondral in nature; (6) a series of dermal gill coverings; and (7) the shoulder girdle, composed of both types of bones.

The names used for vertebrate bony elements are customarily derived, where possible, from those used in man or other mammals. In the early periods of the study of fish anatomy, connecting links between fish and higher vertebrates were unknown; names were arbitrarily applied to fish bones which appeared to occupy the same general position as their mammalian namesakes, although real identity could not be proved. Today our information concerning the transitional forms from fish to higher types is much greater. The nomenclature used here for fish bones is that suggested by recent discoveries and research and hence will be found to differ considerably from that used in many excellent earlier works on fish skulls. In crossopterygians, closest to land forms, most of the bones can be identified with considerable confidence; lungfishes and actinopterygians, however, show such departures from the crossopterygian pattern that the nomenclature used for them is still an arbitrary one in many instances.

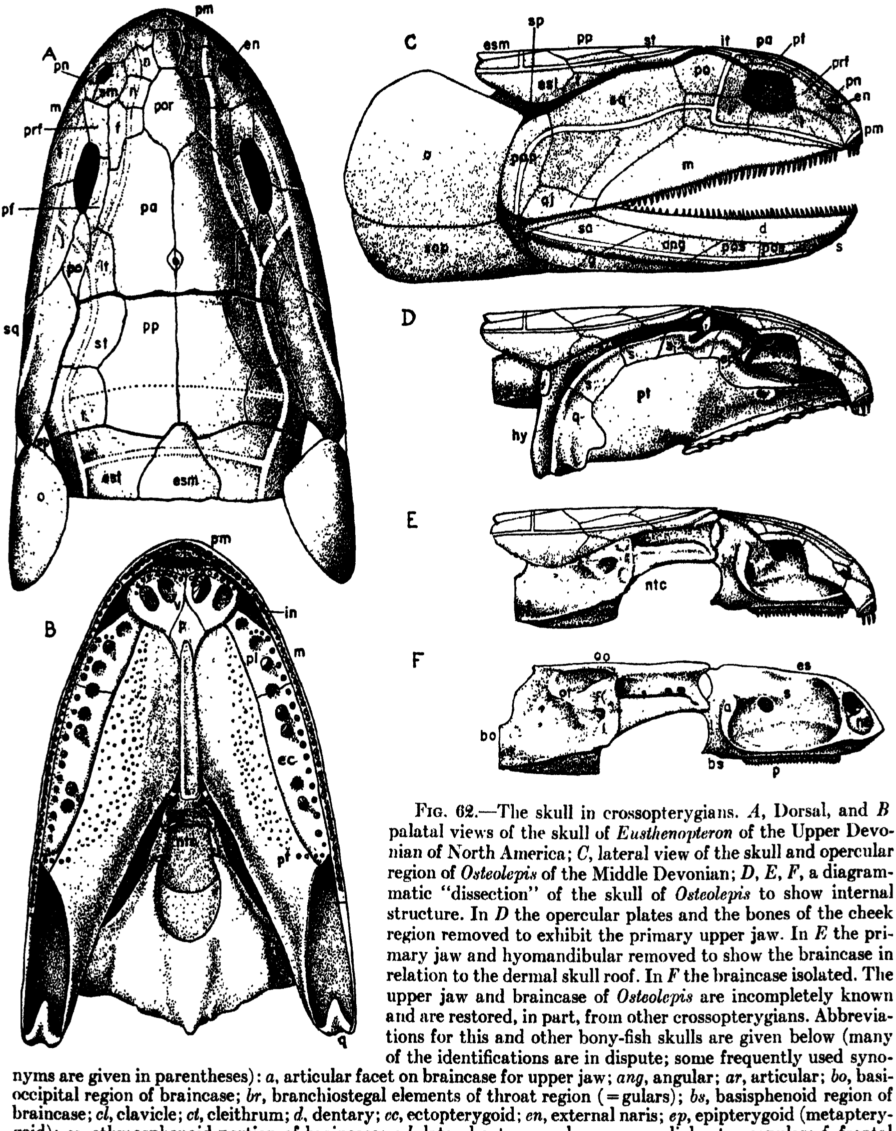


Fig. 62.—The skull in crossopterygians. *A*, Dorsal, and *B* palatal views of the skull of *Eusthenopteron* of the Upper Devonian of North America; *C*, lateral view of the skull and opercular region of *Osteolepis* of the Middle Devonian; *D*, *E*, *F*, a diagrammatic "dissection" of the skull of *Osteolepis* to show internal structure. In *D* the opercular plates and the bones of the cheek region removed to exhibit the primary upper jaw. In *E* the primary jaw and hyomandibular removed to show the braincase in relation to the dermal skull roof. In *F* the braincase isolated. The upper jaw and braincase of *Osteolepis* are incompletely known and are restored, in part, from other crossopterygians. Abbreviations for this and other bony-fish skulls are given below (many of the identifications are in dispute; some frequently used synonyms are given in parentheses): *a*, articular facet on braincase for upper jaw; *ang*, angular; *ar*, articular; *bo*, basioccipital region of braincase; *br*, branchiostegal elements of throat region (=gulars); *bs*, basisphenoid region of braincase; *cl*, clavicle; *ct*, cleithrum; *d*, dentary; *ec*, ectopterygoid; *en*, external naris; *ep*, epipterygoid (metapterygoid); *es*, ethmosphenoid portion of braincase; *esl*, lateral extrascapular; *esm*, medial extrascapular; *f*, frontal (nasal); *g*, gulars; *hy*, hyomandibular; *in*, internal naris; *iop*, interopercular; *it*, intertemporal (postorbital or dermosphenotic); *j*, jugal; *l*, lacrimal (infraorbital); *m*, maxilla; *n*, nasal; *nc*, nasal capsule; *ntc*, area occupied by notochord; *o*, opercular; *oo*, otico-occipital portion of braincase; *ot*, otic region of braincase; *p*, parasphenoid; *pa*, parietal (frontal); *pf*, postfrontal (supraorbital); *pl*, palatine; *pm*, premaxilla; *pn*, postnarial; *po*, postorbital; *pop*, preopercular; *por*, postrostral or internasal; *pos*, postsplenial; *pot*, posttemporal; *pp*, postparietal (parietal); *prf*, prefrontal; *pt*, pterygoid; *pv*, vomer (prevomer); *q*, quadrate; *qj*, quadratojugal; *r*, rostral; *s*, suprapterygoid(s), splenial; *sa*, surangular; *sc*, sclerotic ring; *sct*, supracleithrum; *sm*, supramaxilla; *smp*, symplectic; *so*, suborbital(s); *soc*, supraoccipital; *sop*, subopercular; *sp*, spiracular cleft; *sq*, squamosal; *st*, supratemporal (dermal sphenotic); *t*, tabular (supratemporal-intertemporal); *v*, vomer. (Data in part after Watson, Stensiö, and Westoll.)

The canals which carry the lateral-line sense organs are distinctive features of the superficial elements of the fish cranial skeleton and have rather constant relations to the dermal bones along their courses. The main pair of canals passes forward from the body to the lateral portions of the skull roof (there is typically a cross-commissure between them here) and continues anteriorly to the region above and behind the orbit. A suborbital canal here turns downward around the orbit and forward toward the snout. Another canal—the supraorbital—runs forward above the orbit; in many cases (but not primitively) it connects posteriorly with the main canal. A third major canal curves back and down over the cheek region and then forward along the lower jaw. In addition, there are sometimes rows of pits containing individual lateral-line organs.

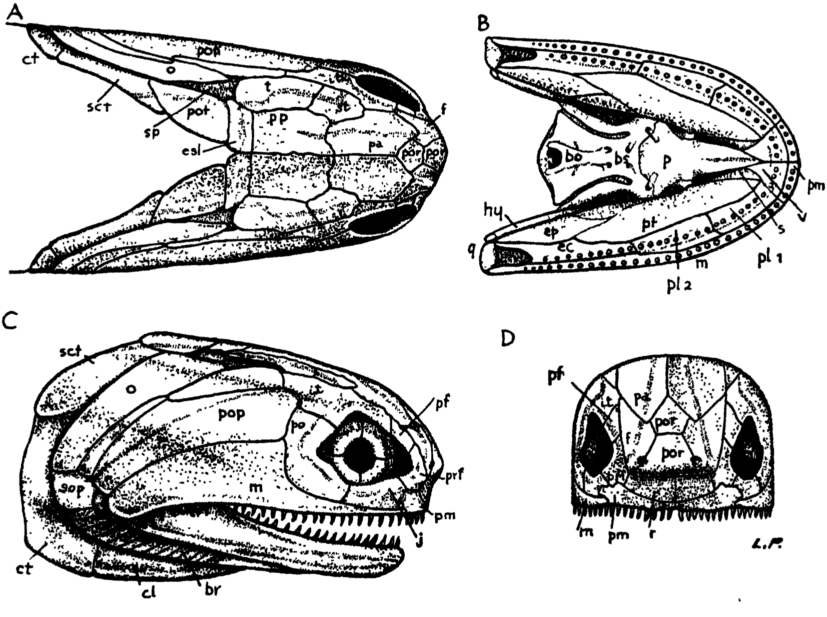


FIG. 63.—*A*, Dorsal, *C*, lateral, and *D*, front, views of the skull and shoulder region of *Cheirolepis*, a Middle Devonian paleoniscoid; about natural size. (After Watson.) *B*, Restoration of the palate of a palaeoniscoid, based mainly upon *Eurynotus*, as described by Watson. For abbreviations see Figure 62.

Dermal bones.—All early bony fishes have a shield of dermal bones forming a nearly solid covering for the top and sides of the head region. The shield is notched posteriorly at either side in the region of the spiracle; its continuity is broken only by the openings for the external nares, the large orbits for the paired eyes, and the pineal opening, when present. The braincase is fused to the lower side of the shield; at its lateral margins the shield carries the principal tooth row of the upper jaw and is in contact here with the palatal structures.

It is probable that in the unknown early ancestors of the bony fishes the skull roof was composed, in the embryo, of a mosaic of small plates. During the evolution of the various groups there appears to have been initiated (more strongly at first in the back part of the skull) a sort of "struggle for existence" among these numerous and probably variable elements, and, as a result, later types have but a few relatively large skull elements. Evidence for such a belief lies in the facts that variable small elements persist in the rostral region of both ray-finned fishes and crossopterygians and that the earliest dipnoans are still largely in a mosaic stage. If this be true, it is likely that we shall never be sure of all homologies between the different bony-fish groups, since it is improbable that the "survivors" have been the same bones in all cases. Nevertheless, a common pattern and grouping of elements can generally be discerned:

1. A variable series of small elements in the rostral region of the skull in primitive forms; usually reduced or much modified in later types.
2. A paired longitudinal series on either side of the dorsal mid-line, typically including, from front to back, nasals, frontals, parietals (bordering the pineal opening, when present), and postparietals (dermal supraoccipitals). The anterior part of this series may primitively occur as a mosaic of small elements at the sides of the rostral region.
3. Marginal tooth-bearing elements—maxilla and, more anteriorly, a premaxilla, which in some cases appears to be a specialized rostral element.
4. A circumorbital ring of bones, in which it is sometimes possible to identify equivalents of the tetrapod elements in this region—prefrontal, postfrontal, postorbital, jugal, and lacrimal.
5. Bones bordering the posterior margin of the skull roof, termed extrascapulars. They appear to be enlarged scales lying beyond the limits of the skull proper and have no homologues in tetrapods.
6. Small lateral elements on the "table" formed by the posterior part of the skull roof and adjacent to the spiracular slit; variable but, in general, corresponding to the supratemporal, intertemporal, and tabular bones of land vertebrates.
7. Elements of the cheek region, sometimes with bones corresponding to the squamosal and quadratojugal of tetrapods, but always with an element, the preopercular, lost in all but the most primitive of land vertebrates.

Dermal bones are also present on the under surface of the skull in the skin lining the roof of the mouth. A median dermal structure, the parasphenoid, lies beneath the anterior end of the braincase. Paired groups of palatal elements supplement and practically replace the embryonic upper-jaw cartilage. These include a large pterygoid bone and a lateral series, frequently of three elements—vomer, palatine, and ectopterygoid, the first functioning primarily as a floor for the nasal capsule. These bones usually are tooth-bearing. This dentition presumably represents that borne on the jaw cartilage of sharks; the lateral tooth row of bony fishes is not represented in elasmobranchs. Behind the ectopterygoid is a fossa through which descend the powerful muscles which close the jaw.

The lower jaw (Fig. 64) consists, for the most part, of dermal bones. The tooth-bearing dentary is a major external element, with bones termed splenial, angular, and surangular below and behind it. Internally a series of dermal elements, which often bear teeth, include a long prearticular, and above it, a series of coronoids.

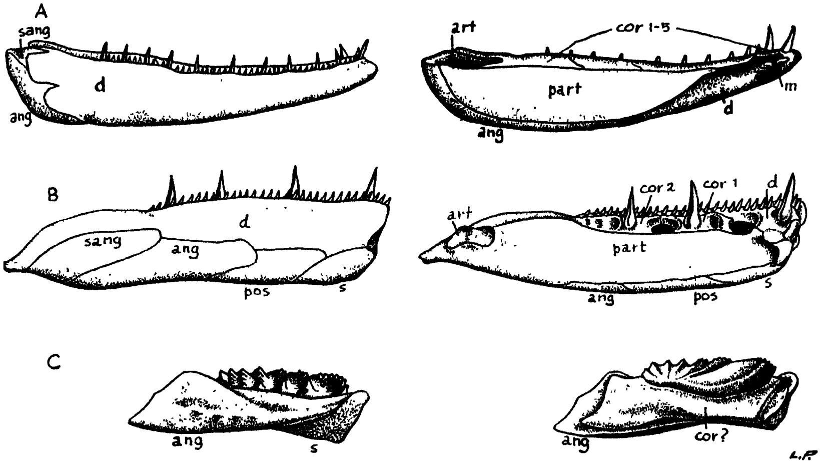


FIG. 64.—The lower jaw in bony fish. Outer view at the left, inner view at the right. *A*, *Nematoptychius* a primitive actinopterygian; *B*, *Megalichthys*, a Carboniferous crossopterygian; *C*, *Sagenodus*, a Carboniferous lungfish (the articular unossified). Abbreviations: *ang*, angular; *art*, articular; *cor*, coronoid; *d*, dentary; *m*, Meckelian bone in anterior end of jaw; *part*, prearticular; *pos*, postsplenial; *s*, splenial; *sang*, surangular. The bone marked *cor?* in *Sagenodus* appears to be the prearticular. (After Watson.)

The gill region is sheathed by opercular elements—laterally a large operculum and suboperculum; more ventrally, in the “‘throat” region, a variable series of gulars, which in advanced actinopterygians become slender rod-like structures, the branchiostegal rays.

The external surface of the shoulder girdle is formed by the most posterior elements of the dermal bone series—a clavicle below (this is lost in higher ray-finned fishes) and a much larger fish element, the cleithrum. The girdle is joined to the table of the skull by supracleithrum and posttemporal.

Replacement bones.—A braincase corresponding rather closely in its form to that seen in early sharks is present in primitive bony fishes as a highly ossified structure. Dorsally the braincase is tightly bound to the dermal bones of the skull roof. Laterally it appears to have been movably articulated with the palatal structure by means of a basal process part way back on either side (adjacent dermal elements take part in the articulation). The evidence gained from a study of the development of living forms indicates that the braincase of the Osteichthyes is composed of a large number of ossifications; in the early types, however, these elements tended to be fused in the adult into larger units, and in some early Osteichthyes the braincase consists of two or three such units, within which there is little or no evidence of subdivision. In later bony fishes, degeneration in ossification usually sets in; cartilaginous areas remain in the adult, and sutures become visible between the bony elements. These structures are rather variable but tend to include (1) a basioccipital and exoccipitals posteriorly (a supraoccipital is present in higher actinopterygians); (2) variable otic ossifications in the ear region, to which the terms proötic, opisthotic, epiotic, sphenotic, pterotic, and intercalar are commonly applied; (3) a basisphenoid in the region of the basal articulation; (4) more anteriorly a tubelike structure comparable to the sphenethmoid of early land vertebrates, or paired elements to which the mammalian terms alisphenoid, orbitosphenoid, and ethmoid are very arbitrarily assigned.

The cartilaginous upper jaw has been partially replaced functionally by dermal palatal elements, but ossifications in the cartilage are also present, including a posterior quadrate which articulates with the lower jaw and variable suprapterygoid elements, one of which may articulate with the basal process of the braincase and is thus comparable to the epipterygoid of tetrapods. The lower-jaw cartilage is almost completely replaced by dermal elements and usually survives only in the form of the articular bone of the jaw articulation.

The hyomandibular, propping the jaw joint, is typically large and well ossified; the remaining branchial arches are variably ossified.

Postcranial skeleton.—Because generally obscured by the thick scaly covering, the internal skeleton of the body is seen relatively rarely in early bony fishes. Of axial skeletal structures, neural and haemal arches are frequently seen to be ossified, as are ribs in many cases, and basal and radial elements in the paired fins. The vertebral centra in most early fishes remained unossified; in later actinopterygians (Fig. 4) they ossify, generally as spool-shaped structures. In crossopterygians partial or complete ossification may occur in the Paleozoic; in some well-ossified forms the large notochord was bounded by dorsal structures seemingly comparable to the pleurocentra of early land vertebrates and ventral elements comparable to the intercentra of tetrapods (Fig. 94).

The shoulder girdle is a compound structure including the dermal elements described above and a relatively small "primary" girdle, variably ossified, with which the fin skeleton articulates. The pelvic girdle is a small and typically wedge-shaped ventral plate.

Radically different types of paired fins (Fig. 65) are found in the two subclasses of bony fishes. In most actinopterygians the fins have a comparatively broad base with a skeleton consisting of a number of parallel bars of bone or cartilage. This is essentially the structure seen in the cladoselachians. In the actinopterygians the internal skeletal elements are usually short, and there is, consequently, only a comparatively small, scale-covered, fleshy lobe; the greater part of the fin consists of a web of skin stiffened by dermal-fin rays. It is to this feature that the group owes its name.

In contrast, a large lobe is developed in the fins of crossopterygians and lungfish, and the dermal rays merely form a fringe about its margins. This lobate fin is of the type termed an archipterygium, already seen among pleuracanth sharks. Only one stout element articulates with the limb girdle. Beyond this the crossopterygians usually exhibit an irregular branching arrangement—an abbreviate archipterygium. The dipnoans and some crossopterygians, however, have the full archipterygial structure—a leaf-shaped fin, the skeleton of which consists of a long, jointed, central axis with symmetrically placed side branches.

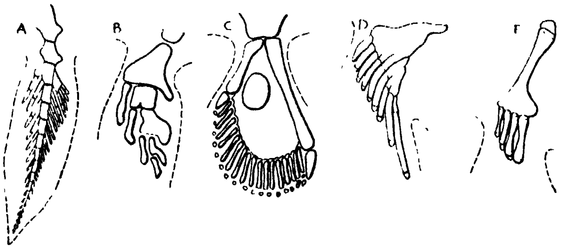


FIG. 65.—The paired fins of bony fishes. Pectoral fins of: *A*, *Epiceratodus*, a modern lungfish; *B*, *Eusthenopteron*, an Upper Devonian crossopterygian; *C*, *Polypterus*, a modern relative of the palaeoniscoids. Pelvic fins of: *D*, the sturgeon, *Scaphirhynchus*; *E*, *Polypterus*. (Mainly after Goodrich.)

The fins of sharks are stiffened by long, slim, horny rays. In bony fishes these structures may be present but are much reduced. The fleshy lobe of the fin is covered with scales, and in addition the remainder of the fin is stiffened by fin rays composed of long, slim, modified scales arranged in rows. Such rays are present both in paired and in median fins.

Lungs.—Gills, never more than five in number, are always present, covered by an operculum and opening by a common slit just in front of the shoulder region. In addition, a spiracle appears to have been present in primitive types but is lost in most recent bony fishes. However, lung breathing, which we naturally associate only with land forms, had its beginning early in the history of bony fishes (Fig. 66) and may have developed even earlier in vertebrate history.

Probably the most generalized condition of the lung is that found in the primitive living actinopterygian, *Polypterus*, in which there is a simple bilobed sac opening out of the bottom of the throat and situated on the under side of the chest in the position of lungs in land animals. It is probable that a similar type of lung existed in the extinct crossopterygians, and a functional lung is present in all the three living lungfish.

The explanation of this unexpected development of lungs in water-living forms is suggested by the habits of the living types mentioned above. These live in regions (such as the upper reaches of the Nile) in which there are alternate periods of rain and drought. During the wet season, lungs are useless; but, with the drying-up of streams, with water present only in stagnant pools, ordinary fish die by the myriad, while those which have lungs may survive until the next rains. Devonian bony fish, as far as we can tell from the sediments, appear to have lived under quite similar conditions, in fresh-water streams and lakes which were subject to periodic droughts. Lungs were a considerable asset to them under these circumstances.

But lungs had obvious disadvantages. They seem to have lain originally in the under part of the chest and would have tended to make the fish top-heavy. In relation to this fact we find that in the lungfish the lung has shifted around to the top side of the body, although its duct may still be attached to the bottom of the throat. And in all the remaining living fishes we find that the lung, or air bladder, is present as a single sac which grows out from the upper side of the throat.

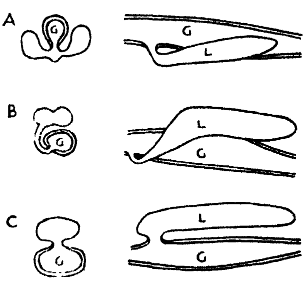


FIG. 66.—Diagram to show the development of lungs in fish and tetrapods. *Left*, cross-sections of gut and lungs; *right*, longitudinal sections. *g*, Gut; *l*, lung. *A*, Paired ventral lungs, found in tetrapods, African and South American lungfish, and *Polypterus*; *B*, lung dorsal but duct ventral, as in Australian lungfish; *C*, single dorsal lung—air bladder—with dorsal duct, as in most actinopterygians.

While a lung is a useful adjunct under the peculiar conditions which we assume to have been present generally in the Devonian and which still exist in a few regions today, it is of little use under more normal climatic conditions. In most living fishes (actinopterygians) the lung has almost entirely lost its original function. But the structure is not lost; it has merely been changed to serve its possessor in another and highly useful way. It is present in most living fishes as the air bladder, a hydrostatic organ. By filling or emptying this sac, the specific gravity of the fish is altered, and it is enabled to float higher or sink lower in the water.

In lower vertebrates the nostrils are simply sacs opening to the outer surface of the head. In land types there is, as well, an internal opening of the nostrils into the roof of the mouth. Such internal openings are not present in any known actinopterygians, but in the Choanichthyes, as the name implies, internal nostrils, or choanae, were early developed and permitted the intake of air into the lungs without the necessity of opening the mouth and running the risk of "shipping water."

Bony-fish ancestry.—The appearance of the bony fishes in the geologic record is a dramatically sudden one. There are no traces of the group in the Silurian and only a few fragments which may be of Lower Devonian age. In the Middle Devonian they appear full-fledged and diversified and at once dominate the scene. The initial stages in their development must have taken place long before, quite probably in the upper reaches of river systems from which no deposits have been preserved.

The common ancestor of the bony-fish groups is unknown. There are various features, many of them noted above, in which the two subclasses of bony fish were already widely divergent when we first see them—features such as fin structure, scale structure, presence or absence of internal nostrils, etc. So marked are these differences that it has been suggested that the Osteichthyes are an artificial assemblage and that ray-fins and choanates represent two separate groups of progressive fishes. However, this is at present mere speculation, and it may be that some common ancestor existed in the waters of late Silurian or earliest Devonian times. Such an ancestor would, of course, have advanced over the placoderms in the development of hyomandibular jaw support and spiracular specialization. Apart from this, the major features of bony-fish organization are to be met with among the placoderms and particularly in the acanthodians. These fishes, for example, show a rather comparable set of complex cranial structures, and there are specific resemblances to the actinopterygians in scales and other characters. The known acanthodians are, of course, too specialized in various respects to be in themselves ancestors of the Osteichthyes. But belief in the descent of the later bony fishes from unknown placoderms closely related to the acanthodians is extremely reasonable.

Ray-finned fishes.—Of the two major groups of bony fishes, the Actinopterygians perhaps merit first consideration because of their seemingly more primitive nature and because the ray-finned fishes, although comparatively rare at the first, were destined to play the chief role in fish history. Today only four genera of choanate fishes survive, while modern representatives of the Actinopterygii are to be numbered by the thousands. In the early days of the study of fishes, the living ray-finned forms were divided into three groups—Chondrostei, Holostei, and Teleostei, in ascending order. The names were based upon mistaken assumptions as to the history of bone development; and today, with a great store of knowledge of fossil forms, we realize that actinopterygian history is much more complex than was once believed. Nevertheless, these three terms still form a convenient framework on which to build a discussion of this vast group and will be used here as superorders within the subclass Actinopterygii: (1) the Chondrostei include the primitive Paleozoic and Triassic types and a few specialized or degenerate survivors; (2) the Holostei were the characteristic ray-fins of middle Mesozoic days and are also near extinction; (3) the Teleostei began their career in the late Mesozoic and have been dominant since the late Cretaceous.

These terms should be regarded as indicating successive grades of development within the Actinopterygii rather than true phyletic units; for, as will be seen, the holostean level of organization was surely attained by more than one group of primitive forms, and the teleosts may be similarly polyphyletic. However, this type of classification, even if not entirely natural, is one which it is best to preserve until our knowledge of the details of the complex evolutionary history of the ray-finned fishes is much more adequate than is the case at present.

There is but a single dorsal fin, in contrast to the choanates. Above the front edge of the dorsals and caudal in earlier actinopterygians are frequently found rows of large V-shaped fulcral scales, forming a protective cutwater for the fins. These are not found in other fish groups and are lost in later ray-finned types.

The scales primitively had the typical ganoid structure; in early forms they were usually rhomboidal in outline. In later types they may be much modified. The shape may change with the development of a rounded or serrate edge (cycloid and ctenoid types of modern teleosts). In most Mesozoic forms the scales lose the middle cosmine layer; the ganoine covering becomes thin in many holosteans and is lost in teleosts, which have simply-built bony scales; and in various cases the entire scaly covering may be reduced or lost.

In the earliest actinopterygians the general arrangement of the bony plates of the head was similar to the generalized pattern described above (Figs. 63, 64). There are, however, marked contrasts with the crossopterygian type characteristic of the choanate fishes. There is rarely a pineal opening; a spiracular slit was early present, but the spiracle was lost in later types; and, most significantly, there is never an internal opening for the nostrils (the story of lung modification in the group is told above.) The orbits are large in primitive actinopterygians, and the large eyeballs are stiffened by sclerotic plates, usually four in number. These forms appear to have relied largely upon vision for their knowledge of the outer world, while most other fish groups appear to place great reliance on the sense of smell. Whereas the mouth is nearly terminal in crossopterygians, it is here preceded by a terminal rostrum in primitive forms. and the external nares in typical actinopterygians are high up on the side of the head, rather than close to the jaw margins. The cheek is mainly occupied in early genera (again in contrast with crossopterygians) by a large preoperculum and an expanded maxilla. A small quadratojugal may be present primitively, but there is no equivalent of the squamosal; there may develop, instead, variable small bones termed suborbitals. From the first, great reliance is placed on the jaw support afforded by the broad hyomandibular element, and in the later ray-finned fishes an extra bone (the symplectic) is added to bind jaw and hyomandibular more firmly. In early actinopterygians the well-ossified braincase often includes three units—an occipital region at the back, paired otic structures on either side, and anteriorly a single mass of bone (sphenethmoid) extending forward to the nasal region. The last two, and in many cases all three of these portions, may fuse to give a very solid structure, contrasting with that described later for the Crossopterygii.

The tail was heterocercal in the oldest-known actinopterygians, as was also the case in early choanates; but it differed in that there was practically no development of fin membrane above the backbone. In consequence, almost never has a member of the present group been able to develop a diphycercal tail—an evolutionary process in which an upper lobe (here generally nonexistent) must be greatly developed to equalize the lower one. A similar result, however, has been attained by the development of a homocercal tail (Fig. 3,*D*), a superficially symmetrical type found in the teleosts, in which the lower lobe only is concerned but in which the scaly tip of the tail is reduced and no longer projects outside the rounded posterior termination of the body. The final result is a tail fin externally somewhat like the diphycercal one but constructed in a very different way.

In contrast with other bony fishes, there is usually little extension of the flesh and internal skeleton into the paired fins (Fig. 65, *D*, *E*), which are mainly supported by long dermal rays. The internal skeleton of the fins consists generally of a number of short parallel bars of bone which may articulate directly with the girdle, although there may be some development of an axis. In the most primitive actinopterygians the paired fins appear to have extended rather stiffly outward from the body as fixed planes, much as in cladoselachian sharks; in later types, with reduced heterocercal tails and consequent changes in swimming habits, the fins become narrower at the base and much more flexible in movements.

Within the actinopterygians there are, in later days, great modifications in the cranial pattern. Ossification may be reduced in various ways. Particularly noticeable is a series of changes in the cheek region, in the course of which, as noted later, the maxilla is much reduced and may even be eliminated from the mouth. The braincase, even if well ossified, tends to retain, in the adult, sutural lines between the numerous bones of which it is composed.

Many of the skull elements in actinopterygians were early named in accordance with their seeming resemblance to elements in the skull of mammals or other tetrapods; additional names, frequently compounds, were added to this artificial system to take care of the numerous variations in pattern. In our illustrations here we have named the actinopterygian skull bones in accordance with the most recent interpretations of cranial history in vertebrates; the terms used will be seen to differ from those found in much of the literature. A key feature is the fact that the bone customarily called frontal in actinopterygians is actually the homologue of the parietal; the neighboring bones, as well, have been reidentified in the light of this.

Like the other bony fishes, the Actinopterygii appear to have originated in fresh waters, and but few members of the group became marine forms during the Paleozoic. By the end of the Triassic, the main center of actinopterygian evolution lay in salt water. Among the modern teleosts the vast majority are marine types, and a good proportion at least of modern fresh-water dwellers are not "original inhabitants" but have reinvaded the fresh waters from the salt.

Primitive actinopterygians, the palaeoniscoids.—We shall classify as the superorder Chondrostei the groups of ray-finned fishes which are primitive in nature or which have remained on a low structural level despite specializations of various types. Such forms include (1) the order Palaeoniscoidea, truly primitive forms, mainly Paleozoic; (2) Subholostei, progressive Triassic types structurally transitional to the holosteans; (3) Polypterini, living African fishes retaining much of the original palaeoniscoid structure; and (4) Acipenseroidea, degenerate modern types.

Early actinopterygians appear, together with crossopterygians and lungfish, in Middle Devonian fresh-water deposits. Rare at first, they so increased in numbers that by the beginning of the Carboniferous they were already the commonest of fresh-water groups, and a few rare forms had already invaded the sea. Most of the more characteristic Paleozoic ray-fins were once assigned to *Palaeoniscus* (properly a Permian genus) or, at the most, were thought to belong to a relatively few closely related genera. In recent decades, however, our knowledge of them has greatly increased, and we now realize that these older actinopterygians include a great variety of fishes which will here be termed the order Palaeoniscoidea. A majority of palaeoniscoids were forms of modest size which at first glance would have resembled in life their actinopterygian successors, the herring- and minnow-like teleosts of modern streams and seas. But there were fundamental differences. The scales were of the thick and shiny ganoid structure, usually with a rhomboidal shape. The tail was heterocercal, and the cranial pattern was that described above as typical of primitive ray-finned forms: large eyes; long mouth gape with a maxilla expanded at the back over the solid cheek, to which was bound a large preoperculum; a well-ossified braincase; a shoulder girdle with clavicle as well as cleithrum.

Despite the similarity in general appearance of many of these fusiform palaeoniscoids, closer study reveals a great variety in structural detail; there is presumably a number of families represented, although the classification is as yet far from settled. *Cheirolepis* (Figs. 63, 67) is the earliest form and a primitive one, notable for the tiny size of its square scales, which give it much the appearance of an acanthodian. *Rhadinichthys* and *Elonichthys* are representatives of a large series of Carboniferous genera with normal body proportions but varied structure; *Acrolepis* and *Palaeoniscus* (Fig. 67) are common Permian types. The primitive genera are long-jawed. In many palaeoniscoids (cf. Fig. 67, *Canobius*) the gape was shortened without bringing about the specializations in construction seen in the later holosteans; a few advanced palaeoniscoids show marked advances toward the holosteans in head structure but are still primitive in other respects.

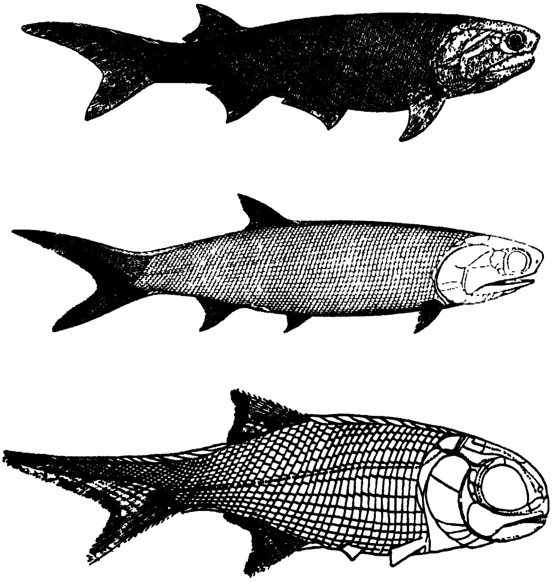


FIG. 67.—Palaeoniscoids. *Above, Cheirolepis*, a primitive Devonian genus, about ⅓ natural size. (After Traquair.) *Center, Palaeoniscus* of the Permian, about ⅓ natural size. (From Traquair.) *Below, Canobius* of the Carboniferous, about natural size. (From Moy-Thomas and Dyne.)

A type of fish found in group after group of actinopterygians is one with a very deep and narrow body, apparently adapted for life in still waters. Such types appeared at an early day among the Carboniferous palaeoniscoids; *Platysomus* and *Amphicentrum* (Fig. 68) are representative of several groups which, it is thought, independently acquired this body shape. *Dorypterus* (Fig. 69) of the Permian shows a strikingly "modern" character in the fact that the pelvic fins have moved forward to a position beneath the throat; this is not found in any other ray-finned fishes until we meet with advanced teleosts in the Cretaceous. It is also notable for a highly modified jaw structure comparable to that seen in later holosteans and teleosts, reduction of scales, and other features suggesting relationship to the later pycnodonts.

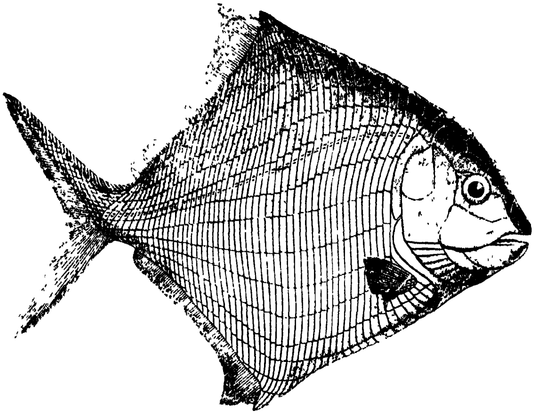


FIG. 68.—*Amphicentrum* (*Cheirodus*), a deep-bodied Carboniferous palaeoniscoid, about ½ natural size. (From Traquair.)

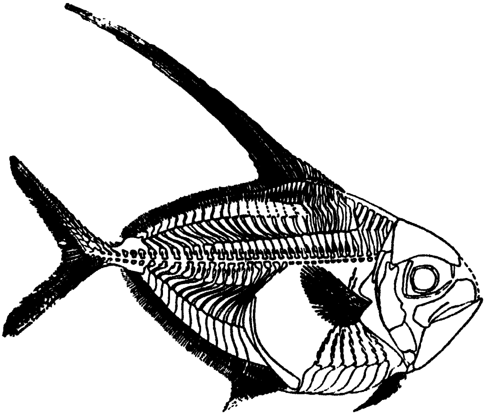


FIG. 69.—*Dorypterus*, an advanced deep-bodied Permian palaeoniscoid, about ½ natural size. (From Westoll, modified after Gill.)

Still more marked specializations appeared in other offshoots of the palaeoniscoid stock, a few of which may be cited here. *Carboveles* (Fig. 70) is a normal form in most respects but has lost most of its scales, retaining patches only on "chest" and tail. *Tarrasius* (Fig. 70) in its cranial structure is a respectable member of the group; but postcranially it not only has undergone a similar loss of scales but has done away with its pelvics and fused its median fins into a long continuous structure analogous to that which has evolved in the entirely unrelated lungfishes.

The Carboniferous was the time of the greatest abundance and greatest variety for palaeoniscoids. In the Triassic the group dwindled rapidly in numbers and variety, for they were being replaced by subholostean and holostean forms evolved from them. A few rare palaeoniscoids, of relatively conservative structure, lingered on into the Jurassic and even the lower Cretaceous before this ancient actinopterygian order became extinct.

Surviving chondrosteans.—Although the palaeoniscoids have been long extinct, they are represented in modern times by a few specialized or degenerate descendants. *Polypterus* (together with an eel-like relative, *Calamoichthys*) is an inhabitant of fresh waters in tropical Africa. The body is covered by thick and shiny ganoid scales—a primitive feature—and the internal skeleton is highly ossified. The median fins are peculiarly developed; the dorsal is represented by a series of small "sails" to which the genus owes its name; and the tail is a nearly symmetrical one. *Polypterus* is remarkable, as has been seen, for the retention of a pair of ventral lungs; their presence may have been influential in the survival of this form in a region subject to seasonal drought.

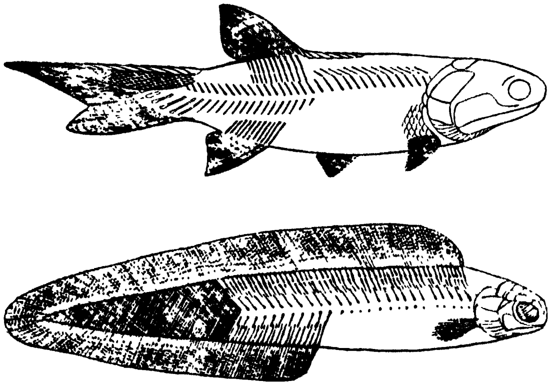


FIG. 70.—Aberrant Carboniferous palaeoniscoids. *Above, Carbovcles*, in which most of the squamation has been lost; about ⅗ size of original. (After White.) *Below, Tarrasius*. Most of the scales are lost, and the median fins are fused into a continuous structure; about ⅔ natural size. (After Moy-Thomas.)

Polypterus is also notable for the presence of a well-developed fleshy lobe in its pectoral fin. Largely for this reason the genus was long thought to be a crossopterygian. But in recent years it has become increasingly apparent that *Polypterus* is, instead, a modified survivor of the palaeoniscoid group.

The scales, when sectioned, show the ganoid structure of actinopterygians rather than the cosmoid plan found in the Crossopterygii; the skull pattern, while modified, shows no crossopterygian structures; internal nares are absent, as is a pineal opening. A somewhat lobate fin may occur in palaeoniscoids; the fin structure of *Polypterus* is closer to the ray-finned type than to that of the choanate fish. All in all, it seems probable that this archaic fish is a modified palaeoniscoid descendant. Connecting links, however, are as yet missing; we know almost nothing of the history of the genus.

More degenerate survivors of the older actinopterygians are the living sturgeons, such as *Acipenser*, and the paddlefishes (*Polyodon*, etc.) of the Mississippi and of Chinese rivers. In these forms ossification has been greatly reduced. In the sturgeon there is but little ossification in the internal skeleton, and the scales have been reduced to a few rows of large bony scutes; the paddlefish is still more degenerate, for there remain only a few small scales at the base of the tail. Head structures, too, have changed greatly, for these bottom scavengers have developed a long rostrum in front of weak jaws. On the other hand, the fins are persistently primitive, and there is a typical heterocercal tail such as is found today in no other bony fishes.

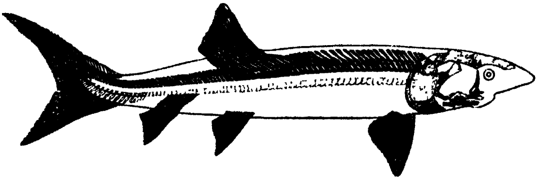


FIG. 71.—*Chondrosteus*, a Jurassic fish intermediate between palaeoniscoids and sturgeons, about 3 feet long. (From Smith Woodward.)

Sturgeon remains are reported from the Tertiary, and paddlefishes are represented by Eocene and Cretaceous forebears. *Chondrosteus* (Fig. 71) of the Jurassic appears to show the transition from the palaeoniscoids; for this fish, while much better ossified than the modern genera, already showed considerable loss of both dermal and replacement bones, loss of much of the squamation, and rostral development.

These forms show the most extreme example of bone reduction to be found among the Osteichthyes. If their evolution had proceeded but a little further, they would have slumped to a purely cartilaginous state comparable to that of the sharks and, in default of fossil evidence, would probably have been considered as primitive cartilaginous fishes—the reverse of the true situation.

Subholosteans.—A very considerable proportion of the Triassic actinopterygian fauna of both fresh and salt water consists of an array of families and genera of fishes which, in both superficial appearance and many anatomical features, resemble the palaeoniscoids and have been generally included in that group. They show, however, various progressive structural trends in which they approach the holostean stage. They may be considered to form an order—the Subholostei—although the group is probably an artificial one. The subholostean families have probably evolved from typical palaeoniscoids through several different lines, and our grouping is an example of "horizontal" classification.

An obvious progressive feature is that the scale-covered lobe of the tail tends to be reduced from the full heterocercal condition; it may become a very slender structure or an abbreviated stub. The scales, although of ganoid type, frequently show the loss of the middle cosmoid layer. There is some reduction in number of the fin rays (cf. p. 96), as in holosteans (and, indeed, in some true palaeoniscoids). In the skull the mouth may be somewhat shortened, but almost never is there any indication of the specialized modifications described below as accompanying gape reduction in true holosteans.

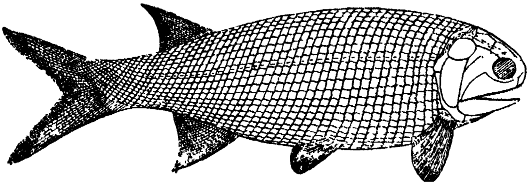


FIG. 72.—*Redfieldia* [*Catopterus*], a Triassic subholostean, original about 5½ inches long. (From Brough.)

The varied Triassic subholostean families show a radiation comparable to that of their palaeoniscoid ancestors in the Paleozoic. The Dictyopygidae (Fig. 72) are a common and relatively primitive family, which shows little departure from typical palaeoniscoid conditions, except that the tail is more or less abbreviated and the rays in the paired fins somewhat reduced in number. The closely related Perleididae exhibit a further reduction in number of rays in the paired fins; the body is holostean in appearance, but the head structure is still palaeoniscoid.

In these and other typical subholostean groups there was obviously considerable variation in habits and environment. The dictyopygids appear to have been mainly fresh-water forms, the perleidids marine. The perleidid *Colobodus* was a large codfish-like form, several feet in length; *Habroichthys*, on the other hand, was a tiny plankton-feeder barely an inch in length. *Dollopterus* had huge pectoral fins suggesting a modern flying fish.

As in the palaeoniscoids, varied deep-bodied types are present. *Cleithrolepis* (Fig. 73), for example, is a form which, except for tail reduction and some modification in fin-ray members, rather closely resembles the platysomids and may not improbably have come from that group. *Bobasatrania*, perhaps likewise a platysomid descendant, is a second deep-bodied form, in which the tail is still fully heterocercal but in which fin-ray reduction, on the other hand, is far advanced and there are apparently marked modifications in the opercular and cheek regions. This form has been suggested as a possible ancestor of the holostean pycnodonts.

The Pholidopleuridae show a curious mixture of primitive and advanced features. In the change of the tail to an almost typical homocercal condition and the loss from the scales not only of the cosmine layer but also of the superficial covering of ganoine, these fishes are as advanced as the teleosts; however, the fins, except the caudal, show typical primitive palaeoniscoid structures, and the skull, except for a few specialized features, is of a palaeoniscoid type.

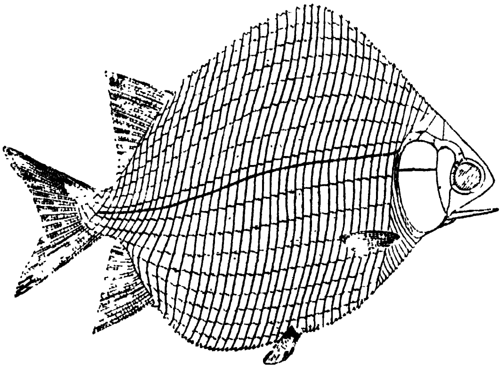


FIG. 73.—*Cleithrolepis*, a deep-bodied Triassic subholostean, about natural size. (From Brough.)

A very specialized holostean side branch, perhaps descended from the last family, is seen in *Saurichthys* (Fig. 74), a long-bodied, long-beaked, sharp-toothed predaceous form. The genus is advanced in the complete reduction of the scaly lobe of the tail, specialized like the sturgeon in the reduction of the scales to a few longitudinal rows of scutes, but primitive in the type of fin rays and in the essential features of jaw construction (although there are special modifications here).

Very advanced types are represented by the early Triassic genera *Parasemionotus* and *Ospia*. The tail is reduced, as is the fin-ray number; the scales have lost the cosmoid layer (although not the ganoine). The jaws are not merely shortened but show structural changes suggesting those seen in the holosteans. Quite possibly they may be actual ancestors of certain of the holostean families.

As has been said, the subholosteans are, in all probability, an artificial assemblage, merely an evolutionary stage reached independently by several lines of palaeoniscoid descendants; but the term is a useful one, to be retained until our knowledge of actinopterygian relationships is on a firmer basis than is the case at present. Presumably, most of the subholostean families were sterile lines, which died out by the end of the Triassic. On the other hand, it is quite possible that some (although not all) of the forms included in the Holostei were derived from subholostean ancestors.

Holosteans.—We shall here group as the superorder Holostei a large, varied, and probably composite assemblage of actinopterygians intermediate in structural features between Chondrostei and teleosts; forms particularly abundant in the middle Mesozoic and represented today only by two American fresh-water fishes—the garpike, *Lepidosteus*, and *Amia*, the so-called dogfish or bowfin.

In the holostean grade of organization are seen, to begin with, the progressive features encountered in many subholosteans. The heterocercal tail is always much abbreviated, and in the more progressive Holostei it gained a superficially symmetrical appearance, but there is not the specialized internal condition characteristic of the true homocercal tail. The scales have lost the middle layer of cosmine, but the superficial ganoine scale-covering persists to a variable degree. Bony fin-ray reduction in the fins is marked. These structures, originally fine, numerous, and segmented along their length, have been reduced to a relatively few stout and unjointed structures, which in the median fins usually correspond in number to the supporting structures of the internal skeleton. The single dorsal air bladder functions slightly as a lung in living forms, although its chief use is hydrostatic. The spiracle has been lost, and in the shoulder girdle the clavicle has disappeared. Ossifications are often developed in the central region of the vertebral column.

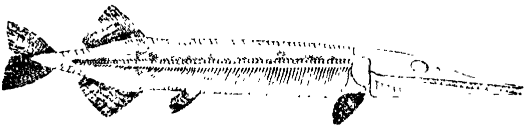


FIG. 74.—*Saurichthys* [*Belonorhynchus*], a predaceous Triassic and Lower Jurassic subholostean, about 20 inches long. (From Smith Woodward.)

It is in the jaw mechanism that distinctive holostean characters are best seen. In palaeoniscoids generally, the mouth opening was elongated, with the jaw joint far back; in subholosteans the jaw articulation frequently moved well forward, but in most cases the essential palaeoniscoid structural features remained unchanged. In the holosteans, however, the architecture of this region is much modified (Fig. 75; cf. Fig. 82). The maxilla is reduced in length, loses its original posterior expansion, and becomes freed posteriorly from the preoperculum (and internally from the ectopterygoid as well). Dorsally, too, the maxilla may be loosened from its original contact with the bones below the orbit; a special supramaxillary element may develop along its upper edge. There is thus initiated a reduction of the maxilla which is to result, in advanced teleosts, in its entire elimination from the functional margin of the mouth. The preoperculum is reduced in size to a crescent forming an anterior margin to the gill cover, and a new interopercular element farther ventrally helps fill the gap left in the throat armor by the forward retreat of the jaws. The orbit is still bordered posteriorly and ventrally by a variable ring of circumorbital elements, but the originally complete covering of the cheek has been lost; this region may be left more or less bare or be covered by a variable series of plates.

With the breaking-down of the cheek region, the entire thrust of the lower jaw must be carried by the internal upper-jaw structures and the hyomandibular; the hyomandibular, the quadrate, and the epipterygoid are all much enlarged as jaw supports, and an extra bone—the symplectic—may unite the quadrate with the hyomandibular.

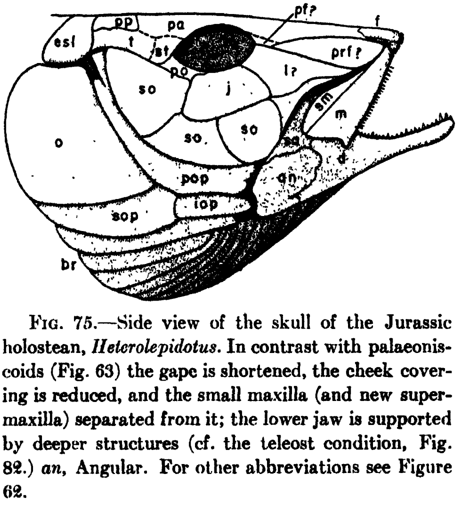


FIG. 75.—Side view of the skull of the Jurassic holostean, *Heterolepidotus*. In contrast with palaeoniscoids (Fig. 63) the gape is shortened, the cheek covering is reduced, and the small maxilla (and new supermaxilla) separated from it; the lower jaw is supported by deeper structures (cf. the teleost condition, Fig. 82.) *an*, Angular. For other abbreviations see Figure 62.

The braincase is known in but few holosteans. In the older holosteans, ossification was fairly complete, but sutural distinctions between regions are generally apparent.

Within the Holostei may be distinguished a number of groups, which we shall here consider as orders. First to appear in time is that represented by the Semionotidae, of which *Semionotus* of the Triassic and *Lepidotus* (Fig. 76) of the Jurassic are typical and common representatives. These are rather heavily built fishes, and *Dapedius* (Fig. 77) is a deep-bodied form analogous to types already seen in earlier actinopterygian groups. The short mouth was armed with peglike or rounded teeth, indicating that some hard type of invertebrate material formed the food supply. The scales in this group are still thick and shiny structures, with a heavy layer of ganoine. The earliest semionotid appeared in the Upper Permian, and hence it is certain that the family did not come from the subholostean assemblage but must have arisen directly from some palaeoniscoid. On the other hand, the specializations in dentition and other features seen in semionotids tend to exclude them from the ancestry of other holosteans.

The modern garpike (*Lepidosteus*)of American waters is usually bracketed with the Semionotidae. The gars, whose pedigree traces back only to the

Eocene, have, like the semionotids, retained thick ganoid scales and exhibit basic similarities to that family in the internal construction of the skull. But they must have had a long independent history, for they are very different

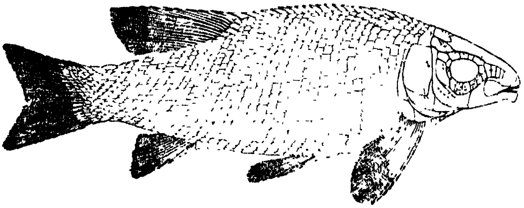


Fig 76.—*Lepidotus minor*, a deep-bodied Jurassic semionotid, original about 1 foot long. (From Smith Woodward.)

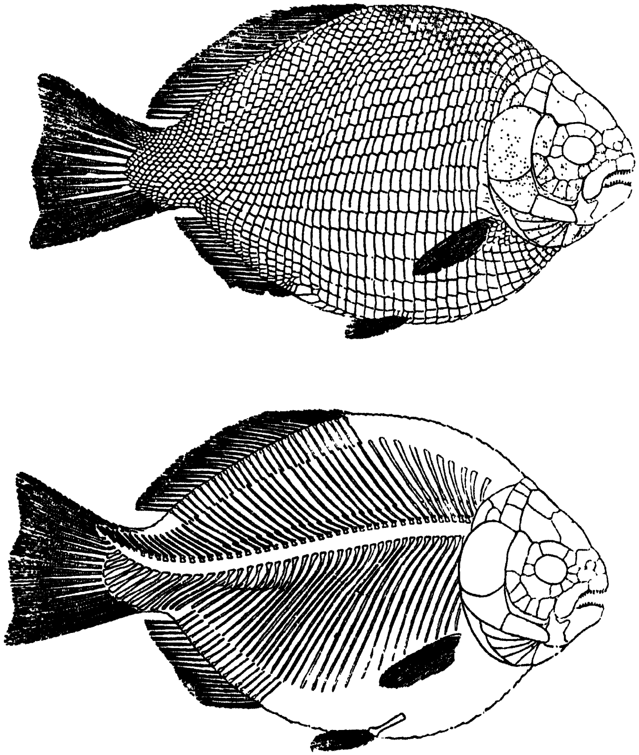


Fig. 77.—*Dapedius*, a deep-bodied Jurassic holostean (Semionotidae), about 14 inches long. (From Smith Woodward.)

in adaptive features associated with predaceous habits. The teeth are sharp, and great elongation of the jaws is associated with marked modifications in dermal bone arrangement. The body, too, is markedly different—long and slim, with dorsal and anal fins far back, and an advanced, nearly homocercal, tail construction.

Aspidorhynchus (Fig. 78) and *Belonostomus* are Upper Jurassic and Cretaceous holosteans which resemble the gars in the retention of thick scales and in body adaptations related to fast-swimming and presumed predaceous habits. However, they show very different cranial structures, which make close relationship improbable, although these fishes, like the gars, are of unknown pedigree. The jaws are moderately elongate; but, in addition, there is developed a long, bony, toothless rostrum, a structure which finds a parallel in other holosteans and teleosts.

A prominent holostean family is that of the Pycnodontidae, including such genera as *Pycnodus*, *Coelodus*, and *Microdon* (Fig. 79)—common in the Jurassic and persisting (in contrast to most holosteans) until the Eocene. In these peculiar forms the body was nearly circular in outline, as in various earlier families, but the appearance was markedly different. Much of the squamous covering of the body was lost or transformed into a latticework of jointed rods. There was a short, deep beak terminating in a tiny mouth filled with pebbly teeth, perhaps adapted for coral-nibbling in the quiet reef waters which may have been a favored environment. The pycnodonts are holosteans in general organization and somewhat resemble the contemporary semionotid, *Dapedius*, in superficial adaptive features. But their specializations show that there is no connection with semionotids or other holostean groups. Again, we must seek a separate pre-holostean origin for these forms, and some of the round-bodied subholosteans appear to be possible ancestors.

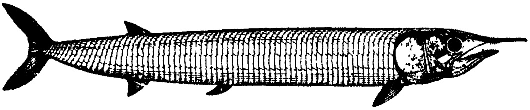


FIG. 78.—*Aspidorhynchus*, an aberrant predaceous Jurassic holostean, about 2 feet long. (From Assmann.)

The typical and central group of holosteans, which we may term (after their sole living representative) the order Amioidea, includes some four families of fishes which dominated the Jurassic seas (fresh-water fishes of that age are poorly known). There are a few Triassic forerunners; very few persisted beyond the Lower Cretaceous. In these fishes we find typical holostean skull structures, with relatively few specializations. The body is generally of a conservative fusiform shape; the tail fin greatly reduced but without any homocercal specialization; the scales still covered with ganoine but becoming relatively thin. The most primitive family is that containing *Caturus* (Fig. 80) and *Eugnathus* [*Furo*]. A small but distinct scaly lobe remains on the tail, and fulcral scales (lost in higher groups) persist; the scales, too, tend here to be rather thicker than in later families. The earliest caturids closely resemble the Parasemionotidae, and caturids (and through them the other typical holosteans) may have descended from this Triassic subholostean group. The Macrosemiidae (Fig. 80) are related forms which tend to develop into somewhat elongate and delicate fishes with long dorsal fins. *Pachycormus* and *Hypsocormus* (Fig. 80) represent a small group in which a heavy bony rostrum developed. In a Cretaceous genus (*Protosphyraena*) this rostrum became much elongated and comparable to that of the swordfishes among teleosts. In relation to rostral support the body has a rather deep, "hump-backed" shape. The fourth family is that of the Amiidae (Fig. 80), represented by Jurassic and Cretaceous genera and by numerous remains of the living *Amia*, or its close relatives, in Tertiary fresh-water deposits. This family has very probably descended from caturid ancestors, but, in addition to the diagnostic feature of an elongate dorsal fin, shows such degenerate or advanced characters as an elongate body, reduction of braincase ossification, thin scales, and development of a nearly homocercal tail.

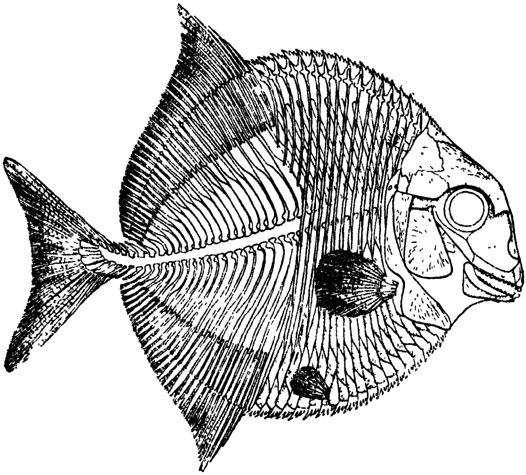


Fig. 79.—*Microdon*, a Jurassic pycnodont, about 5 inches long. (From Smith Woodward.)

A final group of holosteans is that of a series of families—Pholidophoridae (Fig. 81), Archaeomaenidae, Oligopleuridae—which closely approach the teleosts in structural features and appear to be transitional to them. So close, indeed, is the resemblance that some writers include them among the teleosts; and, on the other hand, *Leptolepis* and its relatives, here considered as primitive teleosts, are often bracketed with these families as advanced holosteans. In these forms—small fishes which range from the late Triassic into the Cretaceous—the scales are quite thin, although covered with a film of ganoine, and the tail is close to the homocercal condition. Skull structure in, for example, the development of a supraoccipital element in the braincase is becoming very teleost-like. The ancestors of part, if not all, of the Teleostei may well have been members of this advanced holostean group.

The ancestry of these little forms is none too certain. One would at first assume that they had arisen from generalized holosteans, such as the caturids.

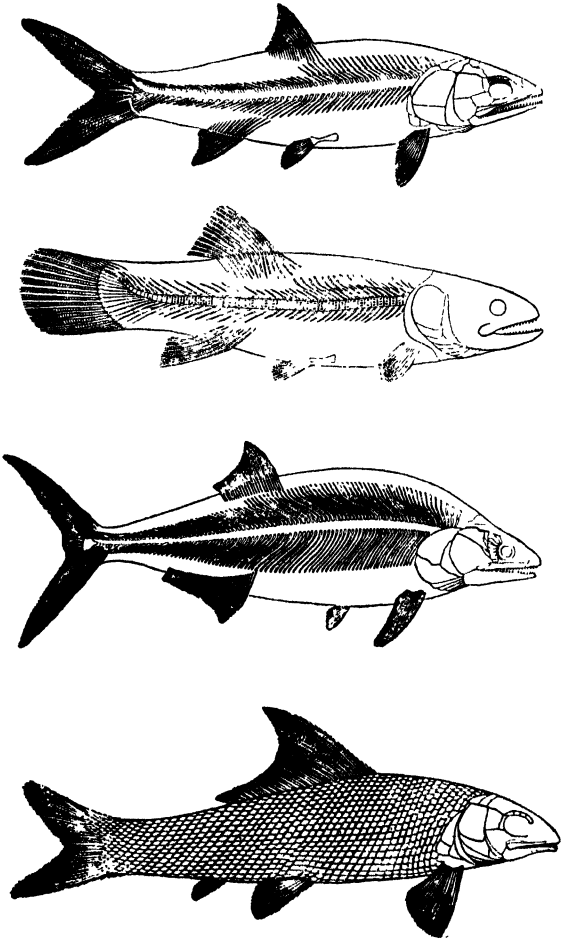


Fig. 80.—Typical Jurassic holosteans of the order Amioidea. In order: *Caturus* (Caturidae) (this and the following much reduced in size); *Amiopsis* (Amiidae); *Hypsocormus* (Pachycormidae), about $\frac{1}{10}$ natural size; *Ophiopsis* (Macrosemiidae), $\frac{1}{3}$ natural size. (From Smith Woodward.)

But some pholidophorids were already present in the Triassic, and these advanced forms may also have arisen directly from subholostean ancestors.

Holostean history is, as we have seen, essentially a Mesozoic story. Except in the case of the semionotids, these forms are unknown until late in the Triassic. By the end of that period they had replaced the subholosteans, and the known fish faunas of the Jurassic and Lower Cretaceous are composed almost exclusively of holostean genera. By Upper Cretaceous times, however, their descendants—the teleosts—had almost completely replaced them. A few pycnodonts remained in the Eocene; in the later Cenozoic only gars and *Amia* remain of this once important group.

As has been seen, the Holostei should be regarded as a structural stage rather than a natural group. The evidence strongly suggests that this stage of evolution was attained independently from presumed subholostean or palaeoniscoid ancestors by different families of the Holostei. The group is thus, in all probability, an artificial "horizontal" assemblage. However, it seems best (as in the case of their predecessors, the subholosteans) to retain this type of classification until their true evolutionary story is better understood.

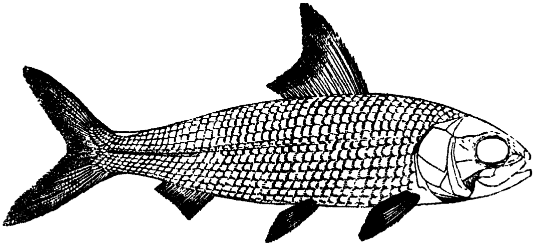


FIG. 81.—*Pholidophorus*, an advanced Jurassic holostean, about 9 inches long. (From Smith Woodward.)

Primitive teleosts.—The teleosts are the successful fishes of today, the culmination of the series of phylogenetic stages seen in the more typical chondrosteans and holosteans. Primitive transitional types appeared in the Lower Jurassic seas and were abundant by the end of that period. In the Cretaceous a wide variety of teleosts was evolved, and by Eocene times every major group of these fishes had appeared. In the Upper Cretaceous they far outnumbered the holosteans, and they have since been the dominant fishes of both fresh and salt waters.

The diagnostic features of the teleosts are merely the further expression of evolutionary tendencies already seen at work in the lower ray-finned fishes. The thin, deeply overlapping scales are so reduced that the shiny ganoid surface layer disappears and the fulcral scales are reduced or lost entirely. The internal skeleton is composed almost entirely of bone, including complete ossification of the vertebrae (in contrast to the usual holostean condition). In the skull (Fig. 82) a supraoccipital bone, small or absent in lower actinopterygians, appears as a new and prominent structure which, in advanced groups, separates the parietals. The vomers are fused into a single median bar. In most groups of fishes, batteries of crushing teeth, when present, tend to form on the palatal bones above and on the inner surface of the lower jaw; in numerous teleosts in which such dentitions develop, the upper tooth battery tends to concentrate on the parasphenoid, while the opposing lower teeth are attached to the bones of the pharyngeal floor. The lower jaw has a reduced number of elements, only the bones termed dentary, angular, and articular persisting. With few exceptions, the median gular has disappeared.

The tail has become homocercal; superficially it is perfectly symmetrical, but internally there is still a trace of the uptilted end of the axial skeleton, and the fin rays are supported by enlarged haemal arches, known as hypural bones. Functionally, this tail is very similar to the diphycercal type attained in other fishes; but here the entire fin is developed from the lower lobe of the original heterocercal tail fin, whereas the diphycercal type is formed equally from upper and lower lobes. The primitive ray-finned forms, as we have noted, almost entirely lacked an upper lobe. The diphycercal type was thus difficult of attainment, but in the homocercal tail the same functional end has been attained by other means.

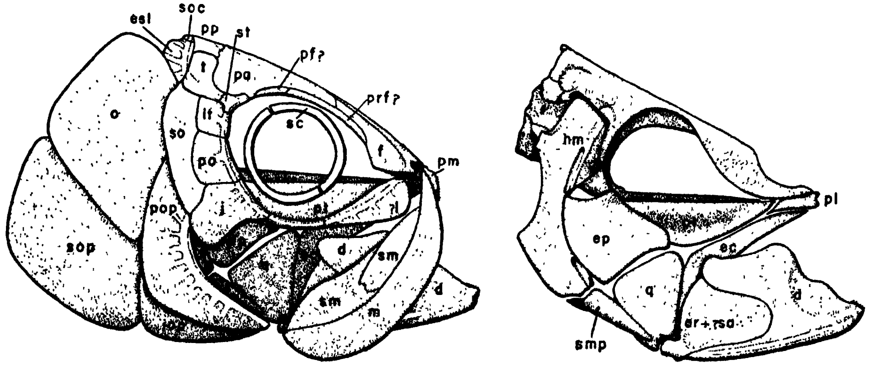


FIG. 82.—The skull of *Leptolepis*. *Left*, superficial lateral view of skull, jaw, and opercular apparatus. *Right*, the dermal bones of the head removed to show the braincase and lower jaw and the support of the latter structure by the palatoquadrate and hyoid elements. *hm*, Hyomandibular. For other abbreviations see Figure 62. (After Rayner.)

Within this group there has been a tremendous amount of variation. Primitive teleosts possessed a normal fusiform body shape; but later members of the group have evolved in almost every conceivable direction—into the elongate eel type of body, into deep-bodied forms paralleling platysomids and pycnodonts, and into such weirdly shaped types as the sea horse. The scales may be lost entirely, as in typical catfish; or the body may be armored, as in other catfish and sea horses, in bony plates, giving a superficial resemblance to some of the old ostracoderms. The fin rays or fulcral scales may be stiffened into spines, as is the case in the higher members of the group. The median fins may coalesce; the pelvic fins in advanced groups tend to move forward and reach a position beneath the shoulder region or even, as an extreme, beneath the jaws. In the upper jaw the premaxilla tends to lengthen and exclude the maxilla from the margin of the jaws. The latter in advanced forms is so articulated that it aids in the protrusion of the mouth, pushing the premaxilla forward when the jaws are opened. The air bladder has lost all trace of breathing function and is purely a hydrostatic organ; and its connection with the gut may be lost altogether, the sac manufacturing gas within its own membranes.

Modern teleosts carry in the liquid-filled sacs of their internal ears tiny calcareous concretions—otoliths, which have characteristic shapes depending upon the varied contours of the membranous sacs in which they are formed. These ear stones are not uncommon as microfossils in various Tertiary clays and give valuable evidence of the presence of forms unknown from ordinary skeletal evidence.

The vast majority of living teleosts are marine in habitat, and so apparently were most of the older-known forms, thus suggesting that the group originated in the sea. Very probably this was the case, but it must be noted that fresh-water fish-bearing deposits are rare in late Mesozoic rocks. A fair number of modern genera dwell in inland waters, and a number (the salmon and eel are familiar examples) divide their time between the two habitats. At the other extreme, many teleosts (particularly, it would seem, "refugee" members of primitive groups) have become abyssal, deep-sea types.

The teleosts comprise not only some twenty thousand or more living species but a vast array of fossil forms as well. How to arrange and classify this huge assemblage is a perplexing problem. Modern students of living fishes have tended to divide the group into as many as twenty or more distinct orders and hundreds of families. We shall not attempt to give any comprehensive account of all the multifarious teleost types but shall content ourselves with a brief review of the character and history of the principal orders and suborders arranged in a somewhat conservative system (cf. Fig. 83).

The more primitive forms, those which have departed least from the structure of their holostean ancestors, may be grouped as the Isospondyli. Their diagnostic characters are mostly of a negative and primitive nature. The fins (in contrast to advanced types) are supported by numerous soft dermal rays; the pelvic fins are in the original abdominal position; the air bladder still has an open duct; the maxilla is of a primitive structure. The earliest-known teleosts were isospondyls; and *Leptolepis* (Figs. 82, 84), a small Jurassic fish, may have been close to the ancestry of the whole order. In this genus and its close allies we have forms which are, in general, teleostean in nature but which exhibit transitional characters. The hypural bones of the tail, for example, were little expanded; and, although the scales are thin, there is still a trace of ganoine on the surface.

The herrings (*Clupea*) and particularly the tarpon are among the most primitive of living isospondyls—the suborder Clupeoidea. The Cretaceous seas were inhabited by a large series of fishes related to these modern types, ranging in size from modest forms to such giants as *Portheus* (Fig. 85), which ran up to a length of 15 feet or more. These early clupeoids very probably include the ancestors of most of the later teleost groups; for example, *Ctenothrissa* appears to be transitional to the advanced spiny teleosts.

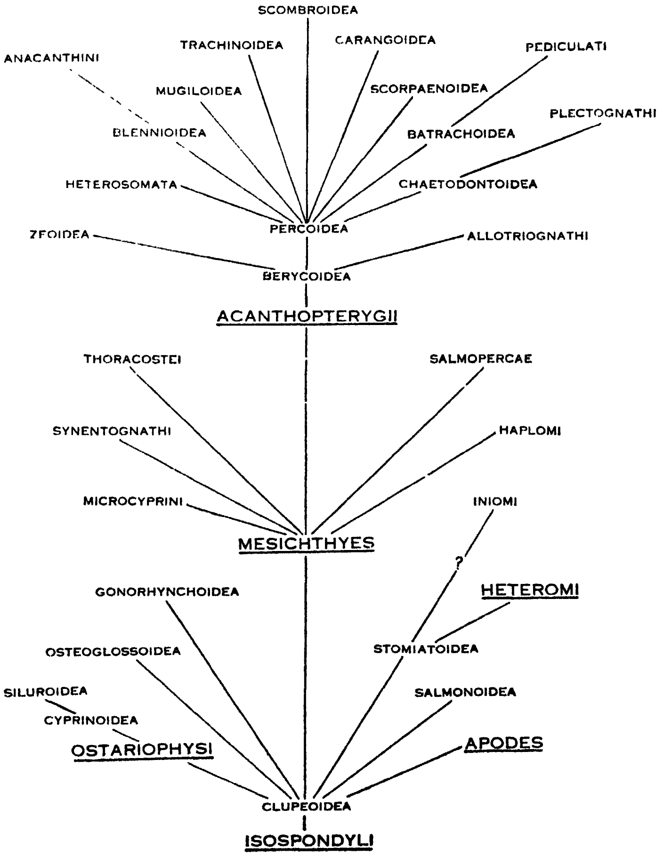


FIG. 83.—A diagram of the arrangement and relationships of the main teleost groups

The salmon and trout are representatives of a somewhat specialized series of isospondyls (Salmonoidea) which live, rather indifferently, in both the fresh and the salt waters of the Northern Hemisphere; some are even deep-sea types. One feature of the group is the presence of a fatty "adipose" fin posterior to the normal dorsal. In some the skull is rather degenerate, with thin bones and a considerable amount of cartilage. We know relatively little of their fossil history, but they were present at least by Eocene times. The Stomiatoidea are voracious, large-mouthed isospondyls found today in the deep seas. Stomiatoids were already present in the Cretaceous; in addition to typical members of the group, there were then numerous examples of an early family of which *Enchodus* and *Eurypholis* (Fig. 86) are representative. Fossil deposits from the deep seas are rare; the early stomiatoids may have been surface fishes whose modern descendants have been forced through competition to seek refuge in the deeps.

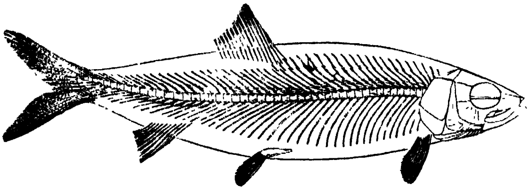


FIG. 84.—*Leptolepis dubius*, a primitive Jurassic teleost, original about 9 inches long. (From Smith Woodward.)

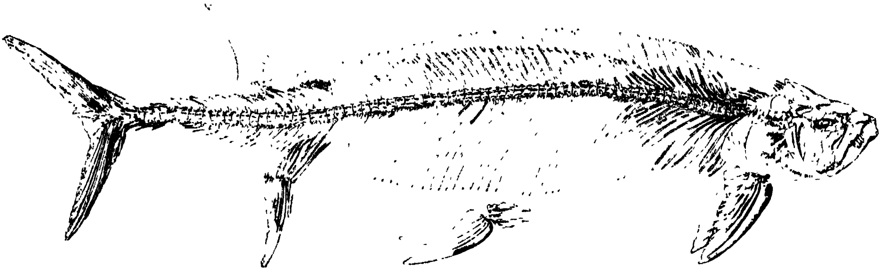


FIG. 85.—*Portheus molossus*, a giant Cretaceous teleost, original about 12 feet long. (From Osborn.)

The osteoglossoids and related types include a number of families of living fresh-water isospondyls with a tendency toward elongate body shape and other specialized features. They are common in South America; moderately abundant in Africa, southern Asia, the East Indies, and even Australia; but almost unknown in northern regions. This distribution is interesting from the point of view of zoögeography and has been used as evidence to support the theory that these southern continents must once have been connected. However, typical osteoglossoids, such as *Phareodus*, are known from the Eocene of both North American and Europe, and hence the present distribution appears to be but the restriction to the tropics of a group once world-wide.

An early side branch of the primitive teleost stock is that which includes the carp and catfish and their relatives, the order Ostariophysi. This numerous group includes a majority of existing fresh-water fishes. A peculiarity is the development of a chain of small bones, formed from parts of the anterior vertebrae and ribs, which run from the air bladder to the ear and appear to be concerned with hearing; this odd structure is in itself sufficient to separate them from the isospondyls. Of the more primitive members of the order, a whole series of families (characins) now inhabits South America but has few fossil representatives. Among northern-continent types, the suckers (catostomids) and loaches (cobitids) are represented by a few Tertiary fossils. The largest family of the order is that of the Cyprinidae, which includes not only the European carp but many hundreds of smaller northern-continent fishes usually termed minnows. Their remains are frequent in Tertiary deposits.

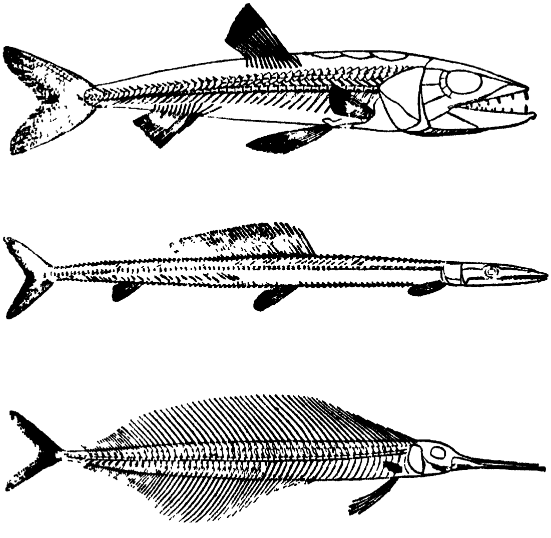


FIG. 86.—Teleosts. *Above*, *Eurypholis*, a Cretaceous stomiatoid, about half natural size. *Center*, *Benthesikyme* (*Leptotrachelus*), a Cretaceous member of the Heteromi, about ⅓ natural size. *Below*, *Palaeorhynchus*, an Eocene scombroid, about ⅙ natural size. (From Smith Woodward.)

The catfishes (siluroids), in which normal scales are absent, are widely distributed today. A few types are present in North America, Europe, and northern Asia; the catfish, however, are mainly found in the tropics, both South America and Africa having numerous genera. Catfish are known from various stages of the Tertiary.

The abundance of Ostariophysi in the southern continents presents a zoögeographical problem similar to that already noted in the case of the osteoglossoids. The origins of the order are practically unknown. Some Cretaceous scales are comparable to those found in primitive Ostariophysi; *Lycoptera*, a primitive Lower Cretaceous teleost from Asia, may be ancestral but lacked the peculiar ear bones diagnostic of the group.

The order Heteromi includes today only a few deep-sea fishes with long heads, long bodies, and long tails on which the true caudal fin has disappeared and has been replaced by a long anal and dorsal. A few typical genera of this group were already present in the Cretaceous, at which time, too, we find possible ancestors in *Dercetis* and related types (Fig. 86), equally long-bodied but with a normal series of fins.

The eels—the order Apodes—resemble the last group in their body elongation; the paired fins are absent in modern forms, the scales are rudimentary or absent, and the upper part of the opercular covering has been lost. These carnivorous fishes have a peculiar, specialized type of mouth structure; for example, the premaxillae appear to be absent and are replaced functionally by the vomers. The group as a whole is marine, although a number of species spend their adult life in fresh waters. Several families of typical eels are known from the Eocene onward; the Cretaceous genera, *Urenchelys* and *Anguillavus*, show rather more primitive conditions in the median fins, and pelvic fins were still present in the latter.

We shall here treat as the order Mesichthyes, or "intermediate" teleosts, a rather artificial assemblage of groups of fishes intermediate in structure between primitive teleosts and the advanced spiny types (Acanthopterygii) discussed below. Most characteristic of their progressive structural features is the tendency for the premaxilla to elongate and exclude the maxilla from the margin of the jaw. The suborder Haplomi includes but a small number of fresh-water forms, which are characterized by the fact that in the large mouth the maxilla, although toothless, still takes part in the gape. The pike, *Esox*, is a familiar representative, and fossil pikes are known from Eocene times on. The suborder Iniomi (Scopeloids) (Fig. 87) are forms from the high seas (many from deep water). They resemble in many respects the stomiatoids among the isospondyls and may have descended from them; however, the exclusion of the maxilla from the jaw margin is a progressive feature. The group appears to be an ancient one, for it was already present in the Cretaceous.

The suborder Synentognathi consists of a rather miscellaneous collection of forms which are, however, held together by technical characters. Included are the needlefishes (*Belone*, etc.), with one or both jaws greatly elongated, and the flying fishes, with much-enlarged pectoral fins. Both types are represented in the Tertiary. The suborder Microcyprini—killifishes and minnows of various sorts—are small fresh-water forms with tiny and often protractile mouths. The suborder Thoracostei contains but a small number of small fishes; among them are such grotesque forms as the pipefish (*Syngnathus*) and the sea horse, while the sticklebacks (*Gasterosteus*) are apparently primitive members of the group. The mouth, again small, is generally at the end of a long tubular snout; the body is elongate and usually incased in bony armor; paralleling conditions in the acanthopterygians discussed below is a tendency for the development of spines on the fins. Several of these curious types were already present in the Eocene. As a final suborder of transitional teleosts we include here the Salmopercae. These comprise only a few genera of obscure North American fresh-water fishes (trout perch, pirate perch) and Tertiary ancestors from this continent. Here there are approaches to the acanthopterygian condition in the appearance of a few spines in the fins and the tendency for migration of the pelvics forward from their primitive position.

Spiny teleosts.—The top rank in actinopterygian evolution is that occupied by the spiny teleosts, here treated as a single large order, the Acanthopterygii, although split into a number of ordinal groups by many workers on recent teleosts. The name is due to the development of stout spines on the dorsal, anal, and paired fins in most of these forms. Even in many rather primitive types a number of the anterior dermal rays of the dorsal and anal fins (perhaps relics of the former fulcral scales) tend to become stiff, unjointed, spiny structures, which in the dorsal fin are frequently set off clearly from the softer rays posterior to them as a more or less independent fin structure. A similar spiny development may take place in the paired fins of the more progressive types. The pelvic fins move forward from the primitive position and lie beneath the thoracic region or even farther forward, beneath the head; the pectoral girdle by its forward movement becomes attached to the cleithrum. The scales become, so to speak, frayed out posteriorly into comblike structures—the ctenoid type, in contrast with the round-edged, cycloid form characteristic of lower teleosts. Although there are numerous variations, the more primitive forms appear to be rather deep-bodied, as in the perch and bass.

The skull becomes much modified. The dermal bones tend to sink beneath the skin and become secondarily covered with scales. The opercular elements frequently bear posteriorly directed spiny processes. As was true in most of the Mesichthyes, the toothless maxilla is excluded from the border of the mouth, and in many cases the premaxilla is so constructed that the mouth is made protrusile.

A few genera of Acanthopterygii appear in the Cretaceous; the group became increasingly important and numerous during the Tertiary. While many of the lower teleosts are fresh-water forms, the majority of spiny forms are marine, and the evolution of the group appears surely to have taken place in the sea. The spiny teleosts are highly varied, but with all sorts of intermediate types between the extremes; as a result they are very difficult to classify, and no uniform or generally accepted system exists. We shall here consider them as a single order but with numerous suborders, which will be listed and discussed in turn.

Suborder Berycoidea, a basal stock of the spiny teleosts. The berycoids are rather deep-bodied, short-headed, and large-mouthed—features which are apparently primitive in the spiny teleosts as a whole. Spines are present on dorsal and anal fins, but not so conspicuously developed as in more advanced groups. Only a few berycoids are present in modern oceans, but, in the Upper Cretaceous seas, *Hoplopteryx* (Fig. 87) and a number of other genera were present. They were almost the only spiny teleosts present at that time.

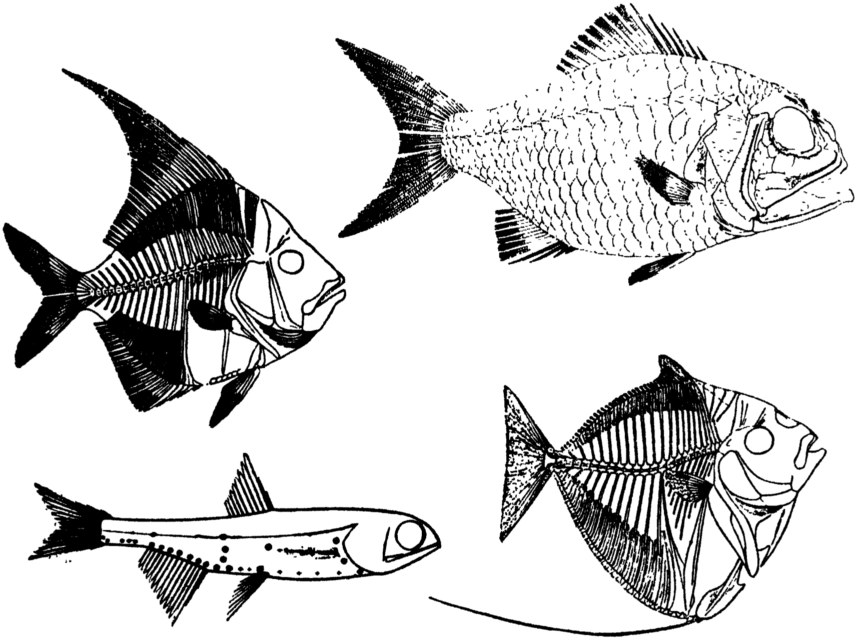


FIG. 87.—Teleosts. *Upper left, Aipichthys,* an Upper Cretaceous carangoid, about ½ natural size. *Upper right, Hoplopteryx,* an Upper Cretaceous berycoid, about ¼ natural size. *Lower left, Myctophum,* a late Tertiary deep-sea member of the Iniomi, about natural size; the spots are remains of light organs. *Lower right,* a fossil carangoid (*Mene*) from the Eocene. (*Myctophum* after Arambourg; others from Smith Woodward.)

Suborder Zeoidea, including the recent John Dory (*Zeus*), boarfish (*Capros*), etc. A small group of thin, deep-bodied primitive acanthopterygians, not clearly marked off from the berycoids; they have been thought to be related to the flounders but are not otherwise of great importance.

Suborder Percoidea, the perches and their relatives, a vast and heterogeneous assemblage including the typical spiny fishes. The fins are well advanced in the development of the spinous condition, and technically they are readily distinguished from the berycoids by the fact that the originally numerous rays in the pelvic fins are reduced to five or six elements. The exact boundaries of the group are difficult of definition. All the more advanced acanthopterygians are, it is generally agreed, derived from the percomorphs, but there is no general agreement as to just which of these fishes should be considered the types of independent groups and which should be left in the Percoidea as a general "catch-all." By some writers one hundred or more families are included. Here we shall use the term in a less comprehensive sense and consider various groups derived from the perches as constituting a series of separate, although related, suborders. Even so restricted, the percoids form an extremely large series of fishes, mainly marine and including such familiar types as perch (*Perca*), fresh-water sunfish (Centrarchidae,) bass (*Serranus*, etc.), snappers (*Lutianus*), porgies (*Sparus*), weakfish (Sciaenidae), and parrot fishes (Scaridae). Only a few percoids were present in the Cretaceous, but they are abundant in the Eocene and later epochs of the Tertiary.

Suborders Scombroidea, Carangoidea (Fig. 87), the most progressive, in many respects, of percoid descendants, which, in the scombroids, tend to abandon the deep-bodied form of the percoids and become speedy swimmers with a long "streamlined" body and a deeply cleft tail. The mackerel, tunny, swordfish, and sailfish (*Scomber, Thunnus, Xiphias, Histiophorus*) are familiar examples of the scombroids. The carangoids, such as the cavallas and pompanos, are less specialized and rather deep-bodied representatives. As with the percoids, these forms are almost unknown in the Cretaceous but abundant throughout the Cenozoic.

Suborder Trachinoidea, the weavers and related fishes. They are slender, long-bodied types, with elongated dorsal and anal fins and with the pelvic fins placed somewhat in advance of the pectorals—the "jugular" position of these fins. There are a score of living marine families of this group, but they are little known as fossils.

Suborder Blennioidea. Similar in most features to the last suborder, the blennies typically are small fishes frequenting rock pools along the ocean shores. The pelvic fins are much reduced, but the pectorals are large and in some cases are used to enable the animal to skip or clamber among the rocks. Again, as with the trachinoids, there is a wide diversity of living forms but only a scattering series of Tertiary fossil records.

Suborder Anacanthini. Probably from blennioid ancestors have come the codfish and related forms. In almost all characters these fishes are typical acanthopterygians; and in their elongate body with tapering tail, long dorsal and anal fins, and small "submental" pelvic fins beneath the chin, the codfishes are seemingly close to the blennioids. A stumbling block to a belief in the descent of the Anacanthini from blennioids has, however, been the fact that (as the name implies) the cods have soft-rayed fins, with, at the most, only a slight development of spinescence in the dorsal. It is, however, possible that the absence of spines is a degenerate, rather than a primitive, feature. Fossil codfish skeletons are rare, but otoliths, at least, occur in a number of Tertiary formations.

Suborder Chaetodontoidea, including the butterfly fishes (*Chaetodon*), angelfishes (*Holacanthus*), and other gaily colored types frequent in the still waters of coral reefs. The body is very deep, the mouth a small but powerful nibbling apparatus. These forms are close to the percoids and are often included with them; their fossil record carries back to the Eocene.

Suborder Plectognathi. We shall use this term to include broadly a varied series of specialized fishes which may well be derived from a primitive chaetodont stock. The mouth is, as in chaetodonts, tiny, but the jaws are nevertheless powerful and armed with heavy teeth. Remarkable among teleosts is the fact that the upper jaw gains extra strength by fusion with the braincase. In contrast to chaetodonts, the mouth is at the tip of a snoutlike prolongation of the skull far in advance of the orbits, thus giving a "horse-faced" appearance to the head. The pelvic fins tend to disappear. In advanced plectognaths—the sclerodermis—there are further specializations. In a series of families of which the modern triggerfishes (*Balistes*) and filefishes are representative and which range as far back as *Stephanodus* in the Upper Cretaceous, an anterior spine of the dorsal fin becomes greatly enlarged and sometimes serrate or movable. Other specialized types are the trunkfish (Ostraciidae), in which the stout body is secondarily incased in armor; the puffers (Tetraodontidae), capable of enormous body distention; the porcupine fishes (Diodontidae), with a spiny armor; and the oceanic sunfishes (Molidae), in which the body is so short that the fish appears to be merely a large deep head. All these families are known in the Tertiary, and all except the last can be traced to the Eocene.

Suborder Heterosomata, the flatfish—flounders, soles, and halibuts. These forms are, in a sense, teleost analogues of the skates, in that they have become flattened bottom dwellers. This, however, has been accomplished in a peculiar fashion. The flatfish have been derived from thin, deep-bodied acanthopterygians which have settled to the bottom on one side, with resulting asymmetrical developments of the new upper and lower surfaces in such features as position of the eyes and structure of the jaws. As with many groups of spiny fishes, the Heterosomata date from the Eocene.

Suborder Scorpaenoidea (Scleroparei), or mail-cheeked fishes and their relatives, including a considerable variety of smaller marine forms, such as the scorpion fishes (*Scorpaena*), sculpins (Cottidae), gurnards (Triglidae), and sea robins. Projecting spines are often present on the opercular and preopercular, and the head may be secondarily armored with dermal bone. A characteristic feature is the fact that the suborbital bones are much elongated and brace the face against the preopercular bone. The pectoral fins tend to be powerful spiny structures. Members of the group are known from the Eocene onward.

Suborder Batrachoidea (Haplodoci), the toadfishes, ugly-looking, flatheaded, broad-mouthed bottom dwellers with powerful armlike pectoral fins. They are unknown as fossils but suggestive of ancestry to the next group.

Suborder Pediculati, the anglers. The group includes various bottom dwellers and deep-sea types which have large mouths and distensible bodies for swallowing their prey whole; they have a most unusual feature in that the first spine of the dorsal fin, overlying the head, carries a dangling tassel or bulb which acts as a lure to prospective victims. Little is known of them as fossils.

The remaining suborders listed are relatively unimportant, aberrant, "odds and ends" of the spiny teleost stock. All (except the last two) are represented to some extent by Tertiary fossil remains. Suborder Gobioidea: small shore dwellers, such as the tropical mudskipper. Suborder Anabantoidea: the climbing "perch" and snakehead, with gill modifications which enable them to survive long absence from the water. Suborder Mugiloidea: mullets, silversides, and barracudas, in which (perhaps secondarily) the pelvic fins are rather far back toward their original position. Suborder Ammodytoidea: the sand lances, small, slender, silvery fishes with toothless jaws. Suborder Echeneoidea: the shark suckers or remoras, with the anterior part of the dorsal fin transformed into a sucking disk. Suborder Xenopterygii: the clingfishes, also with a sucking disk, but one developed on the ventral surface. Suborder Allotriognathi: a small group of marine fishes with varied appearance, such as the deep-bodied moonfish and the slender ribbonfish, but with common diagnostic features, including a peculiar type of small, protractile, and generally toothless mouth. Suborder Opisthomi: spiny-finned fishes paralleling the eels in body shape. Suborder Synbranchii: tropical fresh- and brackish-water fishes, eel-like in form but of obscure relationships, deriving their name from the fact that the gills of both sides open by a common duct. Suborder Polynemoidea: like the mullets but with subdivided pectoral fins.

The history of many other groups of fishes is of interest in connection with the evolution of vertebrates as a whole; that of the later ray-finned fishes has no such interest, for these forms are quite unrelated to the development of further vertebrate types. But for the history of fish alone, no other group can approach them in importance. Since the Paleozoic, almost all other fish groups have tended toward extinction, while the actinopterygians have remained dominant types, and group after group of them has flourished in succession. During the Paleozoic the primitive chondrosteans were the ruling order but have now disappeared except for a few aberrant forms. In the late Triassic and Jurassic the holosteans, their descendants, had taken their place and are found in great abundance and variety. By the Cretaceous the older types had been almost exterminated by the teleosts. Today among the teleosts the spiny types have attained dominance in the seas, the Ostariophysi in fresh waters.

The choanate fishes.—The remaining bony fishes, comprising the Choanichthyes, are, beyond the Devonian, relatively unimportant in their own right but of great evolutionary interest as the stock from which the land vertebrates were derived. The two component groups of this subclass are the Crossopterygii, often termed fringe-finned or lobe-finned fishes, and the Dipnoi, or lungfishes. The Choanichthyes were common inhabitants of fresh waters during much of the late Paleozoic, but today there survive only three tropical lungfishes and a rare, deep-sea crossopterygian.

It is only in recent decades that the close relationship of Dipnoi and Crossopterygii has been realized. The living lungfish are so aberrant (and, we now realize, degenerate) that they were long thought to occupy a position among bony fishes remote from the crossopterygians and ray-fins, and the two latter groups were thought to be fairly closely related. With our present knowledge of fossil forms, however, the historical picture is an entirely different one. As we trace back actinopterygians, crossopterygians, and dipnoans to their first appearance in the Devonian, we find that ray-fins and lobe-finned crossopterygians were then already remote from one another. Lungfish and crossopterygian lines, however, converge as we follow them backward. In the Middle Devonian the early representatives of both groups were not only very similar in general appearance but were also alike in many fundamental characters. These indicated that the two were members of a common bony-fish stock and had diverged from common ancestors not far remote in time or structure.

There are many striking similarities in the postcranial skeleton (cf. Figs. 88 and 92). A heterocercal tail was present in primitive members of both groups of Choanichthyes. This type of tail was also present, as we have seen, in early actinopterygians. There was, however, a seemingly small but potentially important difference. In the ray-fins there is usually no epichordal lobe, that is, no fin development above the body axis. In consequence, when a symmetrical tail developed in later actinopterygians, it had to arise from the lower (hypaxial) lobe alone, as seen in the homocercal tail of teleosts. In the choanate fishes, on the other hand, a small but distinct epaxial lobe was present even in the adult and was presumably large in embryonic stages. When a symmetrical tail was developed (as happened in most later members of the group), this lobe was able to expand, equal the lower lobe in size, and produce a truly symmetrical, diphycercal tail.

A minor but clear-cut distinction between early actinopterygians and choanates is the fact that the older ray-finned genera invariably have a single dorsal fin; crossopterygians and lungfish, two. More important is the contrast in paired-fin construction already discussed. The choanates invariably have an archipterygium of some sort—a full, leaf-shaped structure in lungfish and a few crossopterygians, and an abbreviate archipterygium in other lobe-finned forms.

A fundamental point of agreement between the choanate groups and of contrast with ray-finned fishes lies in the scale structure. Many later choanates have simple bony scales, but in mid-Devonian times both the early lungfish, *Dipterus*, and its crossopterygian contemporaries possessed scales of the cosmoid type described above (Fig. 61). These differ markedly, of course, from the ganoid scales of actinopterygians. Incidentally, this difference in squamation renders highly inaccurate the old-fashioned use of the term "ganoids" in connection with ancient crossopterygians.

Little can be said of the internal bony skeleton in early choanate fishes in general because of the presence of an obscuring scaly covering in many specimens. Of axial structures, many forms show bony neural and haemal arches, ribs, and fin supports. As in actinopterygians, ossifications in the region of the vertebral centra are rare (Fig. 94). They are reported in but one lungfish; in crossopterygians they have been seen in several early genera, in the form of paired half-rings or complete rings perforated for a large notochord; in the crossopterygian *Osteolepis* there are two sets of elements—pleurocentra and intercentra—in each segment, as in many early amphibians.

Certain basic features are present in the cranial structures of both groups. A pineal opening is rarely present in actinopterygians but is common in early crossopterygians, and was present in one archaic lungfish, although it was lost in many later representatives of both groups. The eyes are not so large as in early actinopterygians; and sclerotic plates, when found, are seen to be numerous, instead of limited to four, as in actinopterygians. An important diagnostic feature is the presence of internal nostrils, or choanae, in contrast with ray-fins. In living lungfish, inner and outer openings are not separated by bone but merely by the skin and underlying cartilage. This appears also to have been the case in the older lungfish, where the position of the external nares is indicated by notches, not closed below, in the lower rim of the head shield. A somewhat similar situation is seen in one early crossopterygian; but in most members of that group a stout bar of bone is present below the external opening, as it is in characteristic land vertebrates.

Internal nares are, of course, an excellent adaptation for air-breathing in a water-dwelling vertebrate, and their presence is additional evidence for our belief that functional lungs were present in all early choanates—crossopterygians as well as dipnoans. The presence of these air-breathing adaptations is correlated with the environment in which these fish groups developed. Nearly all the Paleozoic choanates have been found in deposits which appear to be continental in nature. Although some specialized crossopterygians became marine fishes, fresh waters subject to drought or coal-swamp pools similarly deficient in oxygen seem to have been the only conditions under which choanates flourished vigorously.

Both crossopterygians and lungfishes had well-ossified cranial skeletons in the earliest stages of their careers, and certain structural comparisons and homologies of bony elements may be made between them. However, the diagnostic features of the two groups lie in the skull and dentition; they had already diverged markedly in these respects at their first appearance, and their cranial structures are best considered separately.

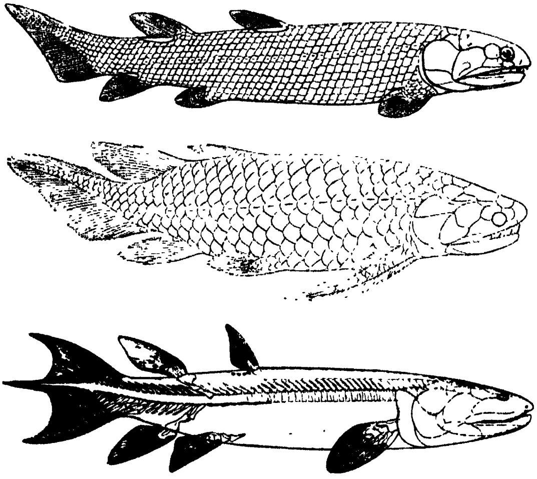


Fig. 88.—Rhipidistian crossopterygians. Above, *Osteolepis*, a primitive Middle Devonian genus, about 9 inches long. *Center, Holoptychius* of the late Devonian, with leaf-shaped appendages comparable to those of lungfishes. Maximum size about 2½ feet. *Below, Eusthenopteron* of the late Devonian, with a trifid diphycercal tail (scales omitted). (*Eusthenopteron* after Gregory and Raven; others after Traquair.)

Primitive crossopterygians.—A few scraps of crossopterygian material, assigned to the genus *Porolepis*, have been reported from late Lower Devonian strata, and we may be sure that the evolution of this important group of tetrapod ancestors was well under way at this time. In the Old Red Sandstone and other continental deposits of the Middle Devonian we find the group represented in abundance and variety. *Osteolepis* (Fig. 88) is the best-known genus of the time and is generally regarded as a very primitive form.

This lobe-fin shows a general structural plan which is repeated, with variations, in a considerable number of other genera of the Devonian and later Paleozoic periods. The body was covered with rhombic scales of typical cosmoid structure. The tail was heterocercal, in presumably primitive fashion. Fully archipterygial paired fins are seen in some crossopterygians, but in the great majority, including *Osteolepis*, there is a short, broad lobe. The internal structure of the fins is not known in *Osteolepis;* in other genera this type of fin contains a much-abbreviated archipterygium. The main skeletal axis is short; side branches are irregular distally, but three prominent proximal pieces appear to be diminutive predecessors of the three major bones of the limb of later tetrapods (Fig. 65, *B*).

In the head region (Fig. 62) both dermal elements and replacement bones are in a highly ossified state. The structures seen in *Osteolepis* and related genera are especially worthy of description because they are preserved with few changes of importance in primitive land vertebrates.

As has been said, the nomenclature of fish bones has been in a confused state, and names familiar in higher vertebrates have been used in an arbitrary fashion. In the last few years, however, evidence has been obtained which enables us to identify with considerable confidence most of the skull elements of crossopterygians in terms of those of tetrapods. This newer nomenclature will be used here.

Most early crossopterygians exhibit a skull covered by a complete shield of dermal bones. The appearance of this shield, however, differs greatly from specimen to specimen. In some the cosmine layer and its shiny, enamel-like surface is widespread over the skull and may superficially fuse large series of elements of the snout and other regions into large plates; in others the cosmine areas are restricted, and all the sutures between individual bones are clearly visible. Such differences were once thought to be of taxonomic value, but it has been reasonably suggested that they represent merely fluctuations, perhaps seasonal in nature, in the lives of the individuals. The fused condition represents periods of stability; the reduction of cosmine allows the elements to separate and growth to occur.

Many of the bones of the crossopterygian skull roof are relatively large and stable structures. Suggestions of the mosaic pattern which we believe to have been characteristic of ancestral bony fishes are, however, seen in the individual variability of the skull pattern in any series of specimens, particularly in the case of the rostral (and postrostral) bones in the center of the snout region. On either side of these structures is a longitudinal row of small elements which collectively correspond to the nasals and frontals of land forms. This row is continued by a pair of plates surrounding the median eye. Their homology was long debated, but they now appear to be the tetrapod parietals, which similarly surround the "pineal" eye. A final posterior pair of elements, occupying half the length of the skull roof, are homologues, despite marked dissimilarity in size, of the postparietals of lower land vertebrates. Back of these is a transverse row of plates, termed extrascapulars, which are absent in land forms and which are perhaps to be regarded as expanded scales rather than as part of the true skull structure.

The margins of the shield are formed by well-developed maxillary and premaxillary elements, bearing a marginal tooth row. Except in one early genus, the two are firmly united and broadly separate the external nostrils from the jaw margin. The naris is sometimes seen to be bordered by one or two small bones, which may correspond in some way to a small bone—the septomaxilla—similarly situated in many land vertebrates. Circumorbital elements are commonly five in number and may be homologous with the five present here in early land forms. A row of bones lateral to parietal and postparietal are, in general, comparable to the similarly situated intertemporal, supratemporal, and tabular of lower tetrapods. In the cheek region the crossopterygians lack the expansion of the maxilla seen in the palaeoniscoids; there is, instead, a large squamosal, as well as a preopercular and a quadratojugal. In palatal view, crossopterygians, like actinopterygians, exhibit a dermal parasphenoid bone covering the lower surface of the anterior part of the braincase; and a set of dermal bones, including pterygoid, vomer, palatine, and ectopterygoid, form most of the palatal surface. The choanae, or internal nares, lie characteristically between vomers and palatines, bounded laterally by maxilla and premaxilla. The lower-jaw dermal elements (Fig. 64) differ in some respects from those seen in palaeoniscoids; there is a large dentary externally, bounded below by a series of four elements, including splenial, postsplenial, angular, and surangular; internally there are a prearticular and three coronoid elements (Fig. 64). Large opercular and subopercular bones cover the gill region laterally, again as in actinopterygians; the ventral gular series comprises a small unpaired median gular, large paired median gulars, and a still more lateral row of small plates completing the armor below the jaws. A well-developed system of lateral-line canals and accessory pitline grooves is present in and on the dermal bones.

The dentition is of particular interest because of peculiar features carried over unchanged into the Amphibia. The teeth are sharp, pointed structures —the crossopterygians were the dominant predators of Devonian fresh waters. Superficially, they usually show longitudinal grooves, which in section (Fig. 89) are seen to represent infoldings of the enamel surface. These folds are often of a complicated nature and cause the term "labyrinthodont" to be applied to this sort of dental structure. The lateral teeth are usually well developed; but, in addition, large fangs as well as smaller denticles are present on the palatal bones and on the corresponding bones on the inner surface of the lower jaw. The fangs are frequently seen to be arranged in pairs, which are replaced alternately so that at least one member of a pair is always functional.

In a number of respects the cartilage-replacement bones correspond to those of actinopterygians. In the lower jaw there is a single replacement element, the articular; a well-developed quadrate opposes it in the upper jaw; although other upper-jaw replacement bones are not so well known, there appear to be suprapterygoid elements, one of which articulates with the basal process of the braincase and may be termed an epipterygoid. There is a stout hyomandibular, articulating by a double head with the surface of the ear region of the braincase.

The braincase is, as in early actinopterygians, well ossified throughout but is highly specialized in certain respects. It was built, in all forms so far investigated, in two distinct units, anterior and posterior, between which a certain amount of motion was possible, at least in many cases. This may have been an adaptation in these carnivorous fishes for taking up the jar caused by a powerful snap of the jaws (articulated to the front part of the braincase) and leaving the posterior segment of the skull (and body) unaffected. The union of the two parts is accomplished not only by articular surfaces but also by the fact that the notochord, almost unrestricted, runs forward through the posterior segment in a large canal beneath the brain cavity and, in life, ended by a union with the hinder end of the front segment. In vertebrates generally, the cartilages which form the braincase are laid down in the embryo in anterior and posterior groups. Here this embryonic division persists into the adult stage; it is notable that many amphibians and reptiles show a zone of weakness in the corresponding position of the adult skull. In *Osteolepis* and various other genera a straight and open suture is present between parietals and postparietals, corresponding to the line of cleavage of the two halves of the underlying braincase. In some individuals, however, this suture is not so marked, and it seems probable that, in general, the movement was not a violent one but merely a "shock-absorber."

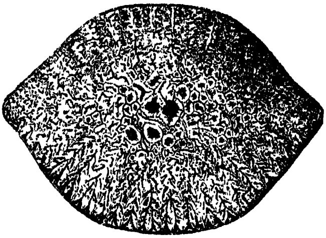


FIG. 89.—Section of tooth of *Holoptychius*, a Devonian crossopterygian, to show the labyrinthine infolding of the enamel. (After Pander.)

A fair number of crossopterygian genera in the Devonian, Carboniferous, and Permian show the typical crossopterygian plan described for *Osteolepis*, but with variations of one sort or another. *Eusthenopteron* (Fig. 88) for example, is a widespread Upper Devonian genus in which the tail had assumed a diphycercal structure with a peculiar trifid outline seen in the later coelacanths. *Thursius* and *Tristichopterus*, likewise Devonian, show transitional stages in body characters; the former resembles *Osteolepis* in most respects and is seemingly closely related to that genus, but the tail is beginning to straighten; in the latter the tail is approaching the trifid condition. *Diplopterax* is a contemporary of *Osteolepis;* but, while suggestively primitive in the presence of incompletely separated narial apertures, has a straight (although not trifid) tail. *Rhizodus* was a giant from the Carboniferous which, in contrast to most members of the group, may have been several yards in length. *Megalichthys* and *Ectosteorhachis* were survivors of this typical group in late Carboniferous and even Permian times. *Glyptolepis* and *Holoptychius* (Fig. 88) show some variation from the typical pattern of early crossopterygian structure. The body was relatively short and deep, with long, slender, paired fins; their general appearance is rather suggestive of the contemporary lungfish. The skull, however, is unmistakably crossopterygian in pattern, although there are differences between these genera and the types previously discussed, such as extra elements in the large cheek and differences in the pattern of the skull table. The internal anatomy is unknown.

The genera so far considered are often grouped in a suborder termed the Rhipidistia. They were, as a group, common in later Devonian and Carboniferous days but had become extinct before the end of the Paleozoic. Their disappearance may perhaps be linked with geological changes which reduced the areas with a stagnant-water type of environment and made lung-breathing of less importance for survival. More important, however, may have been the fact that they were replaced as fresh-water predators by the amphibians, which had arisen from these crossopterygians or forms closely related to them.

Coelacanths.—Much longer lived were the Coelacanthini, a specialized side branch of the crossopterygians. The coelacanths were obviously derived from typical members of the order, but they rapidly evolved a series of specialized and rather degenerate structures. The body, rather stocky in many forms and covered by relatively thin scales, terminated in a three-pronged tail similar to that seen in *Eusthenopteron.* Dorsal and anal fins persisted but became fan-shaped structures with narrow bases; and, while the paired fins, as far as is known, seem to have had a bony structure of the usual crossopterygian type, the scaly lobe was reduced and the ray-supported web increased. In the head the duplex condition of the braincase persisted, but there was a rapid and considerable reduction in ossification after the Devonian, so that most coelacanths show here a series of isolated bony elements with large intervening areas, presumably formed in cartilage. The dermal elements, too, are much modified. There is no pineal opening. The gape of the jaw is shortened, the head becomes short and deep, and the typical development of a sharp angle in the skull outline where the two halves of the braincase join gives these fishes a "Roman-nosed" appearance. The dermal plates of the cheek and gill-covers tend to be much reduced; on the other hand, there are numerous extra "supraorbital" elements along the sides of the snout. Very characteristic is an early reduction and loss of the lateral tooth row except for a cluster of teeth on the premaxillae and the tip of the dentaries; in connection with this, the maxilla and dentary are reduced (lungfish show a comparable history in this regard). The hyomandibular is reduced; and, although the upper jaws still articulate with the braincase, the primitive basal articulation is lost, and a new connection develops more dorsally.

Forms showing a transition to the coelacanth condition are found in the late Devonian, and in the genera *Rhabdoderma* of the Carboniferous and *Coelacanthus* of the Permian the characters of the group were fully established. The early members of the group were, in general, fresh-water types; but in the Triassic, when coelacanths were common and varied, we find them in marine deposits. The group survived in this new environment; *Undina* (Fig. 90) of the Jurassic and *Macropoma* in the Cretaceous are later Mesozoic representatives. It is reasonable to believe that in this environment lung-breathing would disappear; some sort of lung sac persisted, however, for numerous Mesozoic specimens show a calcification in its expected position.

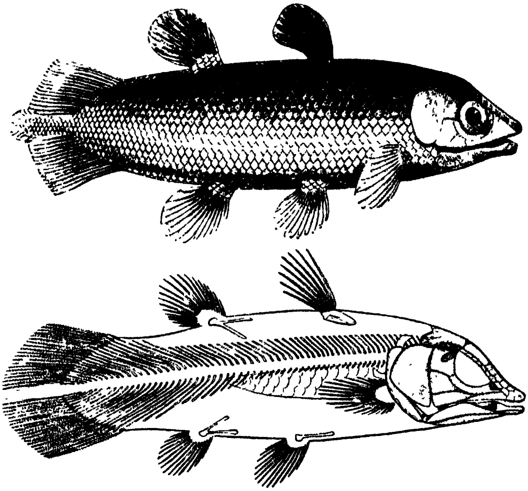


FIG. 90.—*Undina*, a Jurassic coelacanth, original about 22 inches long. *Above*, restored with squamation; *below*, with scales removed. (From Smith Woodward.)

Beyond the Cretaceous there are no fossil records of coelacanths; and it was customary to state, in years past, that the coelacanths (and in them the Crossopterygii as a whole) became extinct at the end of the Mesozoic.

But absence of a group furnishes only negative, not positive, evidence. A few years ago a South African fishing boat, dredging deeper than usual, brought up an unfamiliar fish which proved, to the astonishment of the scientific world, to be a surviving coelacanth, looking in life very much like the restorations of its Mesozoic forebears. The coelacanths had shifted, during their evolution, from fresh waters not merely to salt but finally to the deep-sea regions little represented in fossil deposits of any age. Of this fish (named *Latimeria*) little but the skin was saved, and no other specimen has as yet been found. Better material should yield interesting information concerning the structure of crossopterygians. But we must not expect this coelacanth to have retained very many of the features of its remote ancestors, for its marked changes in life-habits and environment have surely been accompanied by equally marked changes in structure and functions.

Lungfish.—The lungfish, the order Dipnoi, are an aberrant offshoot from the early crossopterygians. When first seen in the Middle Devonian, the dipnoans had already acquired characteristic specializations in skull and dental structures but showed, as has been noted, many fundamental resemblances to crossopterygians. In the late Paleozoic and Triassic, lungfish were moderately abundant and varied in the fresh-water environment in which they arose and to which they were adapted. In later days, however, their fossil remains become rare, and they are represented today by only three tropical forms.

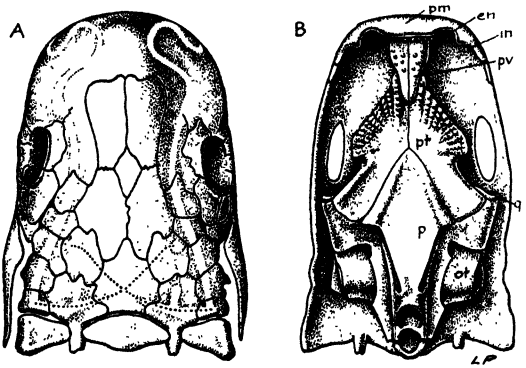


FIG. 91.—*A*, Dorsal, and *B*, ventral, views of the skull of *Dipterus*, a primitive Devonian lungfish. The homology of the dermal roofing elements is in doubt, and hence these have been left unlabeled. Anterior part of braincase, including nasal capsules, unossified. For abbreviations see Figure 62. (After Pander, Watson, and Goodrich.)

Dipterus (Figs. 91, 92) of the Middle Devonian is one of the oldest-known and most primitive lungfish. The body appears fundamentally similar in construction to that of the contemporary crossopterygians. In *Dipterus* two dorsal fins were present and a heterocercal tail like that of *Osteolepis*. In later types the median fins became much modified, the first dorsal disappearing and the second spreading back to join the caudal. Meanwhile, the tail fin had tended to straighten out and fuse with the anal, so that in the living forms there results a continuous symmetrical diphycercal fin bordering the posterior part of the body.

The paired fins in *Dipterus* and all well-known fossil forms are leaf-shaped structures similar to that in the modern Australian lungfish. The internal skeleton is unknown in fossils generally but was presumably of the typical archipterygial pattern found in the modern genus, with a central axis and numerous short side branches. The scales and head plates in *Dipterus* were of the cosmoid type seen in contemporary crossopterygians. In later types the body scales, with loss of the enamel and cosmine layers, tended to become thinner and larger.

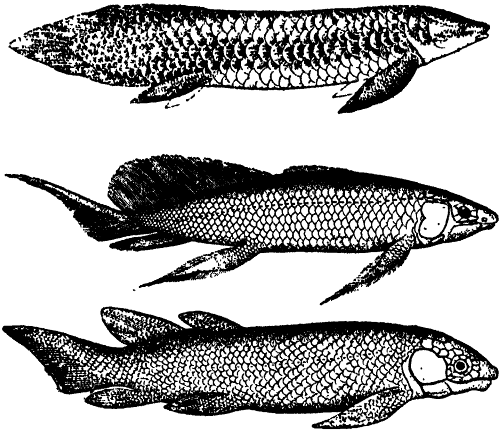


FIG. 92.—Dipnoans. *Below, Dipterus* of the Devonian, primitive genus with a heterocercal tail and median fins comparable to those of crossopterygians. *Center, Scaumenacia* of the Upper Devonian; the median fins are concentrating posteriorly. *Above,* the Recent *Epiceratodus,* with all median fins fused to form a symmetrical caudal. (After Traquair, Hussakof, Norman.)

The presence of choanae in living lungfish, and presumably in fossil ones as well, is an important diagnostic feature linking lungfish with crossopterygians. Associated functionally with this breathing device is the presence in the recent lungfish genera of functional lungs, comparable in all essentials to those of primitive land animals and to those already described in the actinopterygian *Polypterus.* The presence of similar lungs in the fossil Dipnoi, and in crossopterygians as well, is a reasonable inference.

Modern lungfish live under conditions of seasonal aridity presumably comparable to those under which all the primitive bony fish lived. The Australian lungfish, *Epiceratodus,* cannot survive the complete drying-up of the streams, but in foul and stagnant pools may come to the surface and breathe air. The African lungfish, *Protopterus,* and *Lepidosiren* of South America are able to retreat into a burrow and withstand a complete drying-up of the water; the more highly specialized shape and structure of these two forms suggest that this habit was not one characteristic of the Paleozoic forms.

Despite the important diagnostic features linking lungfish to crossopterygians, even the earliest forms show striking differences in skull and dentition. The dentition, particularly, forms a characteristic "trade-mark" of the Dipnoi. Marginal teeth were abandoned in the earliest days of lungfish history, and only in a very few Devonian and Carboniferous specimens are remnants of such structures reported. In some Devonian genera a partial substitute is found in thickened bony rims at the front end of upper and lower jaws, which appear to have functioned as a cropping device in food-gathering. Absent, too, are teeth on the palatal margins, and evolutionary development was concentrated on the formation of toothplates close to the mid-line of the mouth. The prevomers usually carry small toothplates or tooth-clusters, but the major structures are found on the pterygoids above and prearticulars below. In *Dipterus* these bones carry radial rows of large teeth; in later genera these rows form connected ridges borne on thickened fan-shaped plates; such plates, unmistakable in origin, are the commonest remains of fossil lungfish. This type of plate for shearing and crushing, with upper and lower ridges interdigitating, appears adapted to the dipnoan food supply of small mollusks and other invertebrates.

The oldest lungfish exhibit a skull roof which in great measure is still in the primitive stage of a mosaic of small elements. These are particularly small and variable in the anterior portion of the head; more posteriorly they are larger and more constant, with a tendency for the formation of large median plates. It is obvious that in lungfish the process of mosaic reduction was occurring in a fashion rather different from that seen in crossopterygians, and hence it seems extremely difficult to identify "normal" skull elements in the lungfish pattern (Fig. 91).

There is a strong trend toward skull-roof reduction in the lungfish series. Cosmine and enamel layers may be present in *Dipterus* and some of the other Devonian forms, and there appears to be, as in contemporary crossopterygians, a periodic formation of a solid anterior shield. These outer layers are, however, absent in most later lungfish. In most, the anterior end of the head is bare of dermal bones, the lateral walls are gradually reduced, and in living genera there remain but a few large dorsal plates. Opercular and gular elements, except for a large principal gular, also tend to be reduced. With development of the characteristic lungfish dentition, both upper and lower jaws tend to lose much of their dermal structure; some of the elements absent in later dipnoans are represented in *Dipterus* by small ossicles. The loss of lateral teeth has been accompanied by the loss of the premaxilla and maxilla and by reduction of the dentary and other lower-jaw elements. The lower jaw in later dipnoans includes but three bones—two outer dermal elements, which are probably a splenial and the angular, and internally that bearing the toothplate, presumably the prearticular. The palatine and ectopterygoid have disappeared from the palate.

As in various other fish groups, the lungfish show a marked phylogenetic reduction in the degree of ossification of replacement bones—a reduction more rapid than in any other group of bony fishes and more complete than in any others except the sturgeons and paddlefishes. The braincase had lost almost all ossification, apparently, by Carboniferous times. It was still ossified, posteriorly at least, in a few recorded Devonian specimens. We know little about it, however, except the important fact that it was a single compact structure which lacked the bipartite specialization of the crossopterygians.

The cartilage elements of the jaws and gill arches show little ossification even in early forms. In *Dipterus* the articular and quadrate, forming the jaw joint, were ossified, but even these structures later slumped back to a permanent cartilaginous state. The recent genera show us that dipnoans have changed radically in basic jaw construction from that found in other bony fishes; the primary upper jaws have fused to the braincase, with, of course, reduction of the hyomandibular, which plays a prominent part in jaw support in other groups. This specialization is parallel to that found in the chimaeras and is obviously related to a similar function—strong support for the crushing toothplates.

Much of the description above has been based on *Dipterus*, a primitive form which appears in the Middle Devonian. Among the primitive features to be noted in this genus are the unspecialized median fins, retention of cosmoid scales, and a complete skull shield. An Australian contemporary, *Dipnorhynchus*, is still more primitive (it retains a pineal opening, for example), but is imperfectly known.

From *Dipterus* a "main line" of lungfish evolution can be traced to the living Australian lungfish. In the Upper Devonian genera *Scaumenacia* (Fig. 92) and *Phaneropleuron*, common fishes of their period, the first dorsal fin is much reduced, the second much enlarged and moving backward, and the anal is likewise moving back to a position close to the caudal; in the latter form dorsal and caudal are joined. The Carboniferous genera *Sagenodus* (Fig. 64) and *Ctenodus* are represented mainly by abundant and characteristic toothplates, and the body outline is little known. Some late Paleozoic lungfish, however, appear to have completed the fusion of the median fins into the symmetrical and deceptively simple-looking diphycercal tail seen in the living forms. *Ceratodus* is a genus common in the Triassic, with large, flat toothplates which show little trace of the separate teeth of which they are composed. In later deposits remains are rare; the living Australian lungfish appears to be closely related to the Triassic form, although frequently placed in a separate genus, *Epiceratodus*.

From this central line of dipnoan evolution there have been various side branches. Notable in the Upper Devonian are two genera which became long-snouted types, *Rhynchodipterus* of Scotland and Greenland and *Fleurantia* (Fig. 93) of America. Despite superficial resemblances, the two had evolved independently; the former, for instance, shows great similarity to *Dipterus* in its bodily build, the latter has fins comparable in most respects to those of *Scaumenacia*, and there are important differences in skull structure. In *Fleurantia* there are, instead of well-formed toothplates, merely a few rows of cusps on the pterygoid and a shagreen of smaller teeth; *Rhynchodipterus* is thought to be toothless. A similar reduction of the toothplates appears in the Carboniferous *Uronemus* and *Conchopoma* of the Permian, which, however, seem derived from the *Sagenodus* group and are apparently little specialized in other respects. A final side branch of the dipnoan stock is that seen in the living African and South American genera, *Protopterus* and *Lepidosiren*. In these forms the body is rather long and eel-like, the fins degenerate, and the toothplates reduced to a few shearing ridges. A few late Paleozoic teeth suggest the beginning of this type of specialization, but the story is obscure.

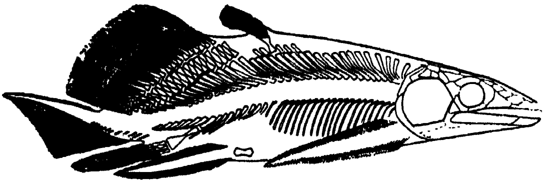


FIG. 93.—*Fleurantia*, a long-snouted Upper Devonian lungfish, about ⅓ natural size. (From Graham-Smith and Westoll.)

CHAPTER 6

AMPHIBIANS

WE NOW turn from a consideration of the fishes—primitive vertebrates for whom water is the natural habitat—to the history of land vertebrates, the tetrapods. These forms have made one of the most radical advances in vertebrate history in the development from fish fins of limbs capable of being used for progression on land. The change from water to land life, first initiated in the Devonian by the ancestral amphibian stock, was completed by the reptiles in late Paleozoic days; later, from reptilian types, were developed the birds and mammals. Once the water was left behind, wide and repeated radiations of tetrapod types occurred. The four-footed vertebrates have adapted themselves to almost every conceivable type of land habitat and have, moreover, taken to the air and, backed by the advances made in land life, have reinvaded the seas. Snakes, birds, men, and whales are but a few examples of the widely varied types which evolved from the primitive and ancient forms which in late Paleozoic times first left the streams and pools to walk upon the land.

Amphibian life.—Most primitive and earliest known of tetrapods are the amphibians, which as a class are, without question, the basal stock from which the remaining groups of land vertebrates have been derived. Living amphibians include but three comparatively unimportant vertebrate groups: the frogs and toads (Anura or Salientia), the salamanders and newts (Urodela), and some rare wormlike types (Apoda). All are highly specialized and have in many respects departed far from the primitive type described below.

The life-history of a typical frog, however, shows the essential characters of the class. The eggs are usually small and without the protective membranes or shell found in the eggs of reptiles and higher types. Typically they are laid in the water, whereas the reptilian egg is laid on land. The young embryo, without any great supply of yolk for nourishment, hatches out at a very immature stage as a tadpole and must find its own food as it grows in the water. Later, when the frog approaches maturity, the structure of the body changes radically; the gills disappear, lungs and limbs develop rapidly, and the animal becomes a land, instead of a water, type.

But the amphibian is not even then freed entirely from an aquatic environment, for the eggs normally must be fertilized and laid in that element. Consequently, the amphibian must return to the water at the breeding season, and complete adaptation to land life alone is impossible. Various devices have been developed by amphibians to help them avoid, to some extent, this necessity for a double mode of life and a double set of adaptations, but never with complete success. It is not to be wondered at that among the salamanders, and apparently among many extinct groups as well, there have been numerous types which have, so to speak, given up the struggle and reverted to a permanent water life and a retention of gill breathing.

The type of reproduction and development is the best definitive feature of the class. For living groups, certain other characters (particularly those of the skeleton) have been used to distinguish the group from the reptiles; but among the fossils practically all anatomical differences break down.

Among existing types the salamanders and newts approach most closely the body form which is probably the primitive one (the frogs, tailless and with elongate hind legs, are among the most highly specialized of vertebrates). The body and tail are elongate; median fins have disappeared; but the tail is often high and flattened and may be used as a swimming organ in rather fishlike fashion. The paired fins of the ancestral fish have been transformed into tetrapod limbs, which in salamanders are usually quite small and feeble as compared with those of reptiles and other higher tetrapods but are quite large as compared with fish appendages. While these limbs are capable of a great amount of independent motion, it is of interest that a salamander progresses more or less in fish fashion on dry ground, the body being thrown into S-shaped curves, which may advance the limbs with very little movement on their own part.

Structure of a primitive amphibian.—But while a salamander may resemble the probable tetrapod ancestors superficially, the internal anatomy of all modern amphibians is very much modified from primitive conditions. The structure of some primitive fossil types will be described below in some detail, since the fundamental pattern of the skeleton of those forms is basic for an understanding not only of the history of later amphibians but of that of reptiles and higher tetrapods as well. Almost every skeletal element of a bird or of a man may be traced back to these primitive types. Later forms have modified the shape and relationships of parts greatly, and there have been frequent losses of bones; but the fundamental pattern laid down in the early tetrapods still persists.

Our description will be based in great measure upon such primitive Carboniferous genera as *Palaeogyrinus* (Fig. 96), *Eogyrinus* (Fig. 108), *Megalocephalus* (Fig. 97), and *Diplovertebron* (Fig. 109), members of the Labyrinthodontia, an important group of primitive amphibians. These types were common inhabitants of the coal swamps. *Diplovertebron* appears to have reached a maximum length of about two feet; many of the older labyrinthodonts were considerably larger. The general proportions were not unlike those of a modern salamander, but the body was somewhat higher and more rounded in section. Most of the life of such an archaic tetrapod was still spent in the water, and the small palaeoniscoid fish, then abundant, may have served as a major source of food supply. There was still much resemblance to the fish type both in structural features and in a continuation of the ancestral aquatic mode of life. But the development of tetrapod limbs, rendering land locomotion possible, is an obvious and striking difference.

Bony scales, present in the fish ancestors, have tended to be reduced in land forms, although horny scales may functionally replace them in reptiles and other types (modern amphibians have a soft, moist skin). Ancient amphibians and some modern reptiles retain the bony scales in a ventral armor of V-shaped rows along the belly, a structure of use in protecting the low-slung body while traveling over rough ground. Traces of reduced bony scales covering the flanks and back are found in some of the older Amphibia, but (except for vestiges in the wormlike Apoda) they have disappeared in living tetrapods, although later reptiles (and even mammals) may redevelop bony armor.

Axial skeleton.—In most of the older fishes the neural arches of the vertebral column were well ossified, as were the haemal arches in the tail; the centra, however, were usually cartilaginous. We have noted that centrum ossifications were present in some crossopterygians; in amphibians this region is highly ossified, for the backbone must carry the weight of the body and cartilage could not stand the strain.

In lower tetrapods the nature of the centra is of great significance in classification. Two fundamentally different types of construction are found among the amphibians. One, of lesser importance, is the lepospondylous ("husk vertebra") type, found in numerous small Paleozoic forms (Fig. 95) and retained today in the salamanders and wormlike amphibians. In this type the centra form directly by the deposition of bone around the embryonic notochord, without preformation in cartilage. They are single structures, often essentially spool-shaped and pierced lengthwise by a hole for the persistent notochord.

More important phylogenetically is a second type ("arch vertebra") found in the larger and more prominent ancient amphibian groups (Fig. 94) and persisting today in one form or another not only in the frogs but in all the higher vertebrate classes as well. This type is a direct inheritance from the crossopterygian one. We have noted that in some members of that fish group each segment of the body contained two sets of centra, laid down as cartilage blocks or arches and then ossified to a greater or lesser degree, the anterior ones termed the intercentra, the posterior termed the pleurocentra.

These structures are characteristically present, although in varied fashion, in a great series of Paleozoic amphibians termed the Labyrinthodontia. Several different subtypes of arch vertebrae are found in this group. In the rhachitomous condition, possibly the most primitive one, the intercentrum in each segment is a median ventral element, wedge-shaped in side view, crescentic in outline as seen end-on; the pleurocentra, which correspond to the true centra of higher classes of vertebrates, are paired, diamond-shaped blocks which fill in the gaps on either side between neural arches and intercentra. The stereospondylous vertebra, prevalent in Triassic labyrinthodonts, differs in that the pleurocentra are reduced or absent and the intercentrum has grown to occupy the entire segment. A different evolutionary development leads to the embolomerous construction common in the Carboniferous. Here both the intercentrum and the pair of pleurocentra have grown to form complete checker-shaped elements pierced for the notochord; each segment thus has two well-formed centra. A fourth pattern is that seen in *Seymouria* and its relatives; the intercentrum is, as in the rhachitomes, merely a large wedge; the pleurocentrum (as in embolomeres) is a major cylindrical element equivalent to the true centrum in the reptiles.

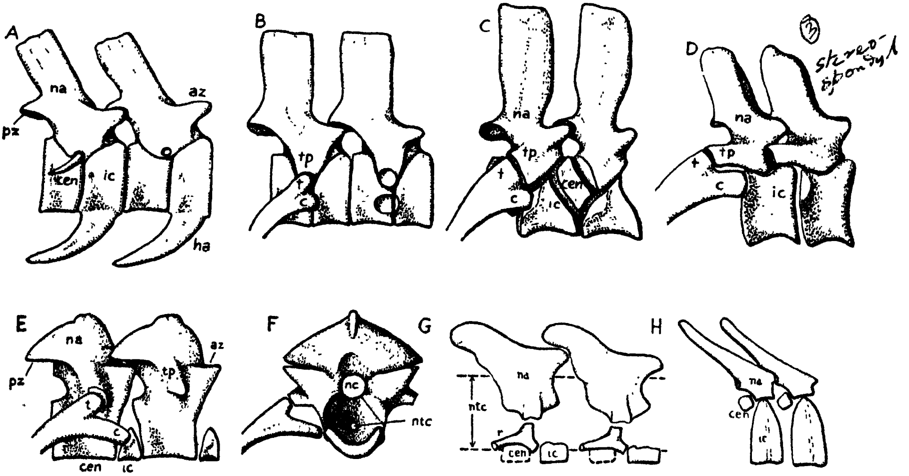


FIG. 94.—The vertebrae of apsidospondylous amphibians. *A*, Caudal vertebrae of the embolomere, *Archeria* ("Cricotus"); *B*, dorsal vertebrae of the same; *C*, dorsal vertebrae of the rhachitome, *Eryops*; *D*, dorsal vertebrae of the stereospondyl *Mastodonsaurus*; *E*, lateral, and *F*, anterior, views of dorsal vertebrae of *Seymouria*; *G*, lateral view of dorsal vertebrae of the presumed frog ancestor, *Miobatrachus*; *H*, lateral view of dorsal vertebrae of the crossopterygian, *Eusthenopteron*. Abbreviations: *az*, Anterior zygapophysis; *c*, capitulum; *cen*, centrum (usually termed pleurocentrum in Amphibia); *ha*, haemal arch; *ic*, intercentrum; *na*, neural arch; *nc*, position of nerve cord; *ntc*, area presumably occupied by notochord; *pz*, posterior zygapophysis; *r*, rib; *t*, tubercle of rib; *tp*, transverse process. (*A–C* mainly after Williston; *D* after von Meyer; *G* after Watson; *H* after Gregory.)

Neural arches are well developed in all land vertebrates. The segments of the column connect with each other not only by juxtaposition of the centra but also by special articular processes—zygapophyses—on the arches. At the back of each arch there is a pair of round, flat surfaces, facing down and somewhat outward. These posterior zygapophyses articulate with corresponding anterior zygapophyses, flat surfaces on the anterior side of the arches, facing upward and inward. In the tail are Y-shaped haemal arches (chevron bones); when intercentra are present, they are formed in common with these arches.

Of the two types of fish ribs, only the dorsal set is present in a tetrapod. Two-headed ribs appear to have been primitive, the true head or capitulum articulating with the intercentrum, and the tubercle meeting a transverse process from the neural arch. However, the two heads tend to be well separated only in the anterior part of the trunk; farther back along the column the heads tend to fuse. Phylogenetically, too, the heads may fuse throughout the column or become variously modified in other ways. The ribs are found along nearly the whole length of the body from the first vertebra in the neck to the proximal part of the tail. The longest ribs are in the thoracic (chest) region, but there is little differentiation of a cervical (neck) or lumbar (waist) region. Opposite the pelvic girdle a specialized rib, the sacral, gives attachment for the girdle in most amphibians; in higher classes there are usually two or more such sacral ribs.

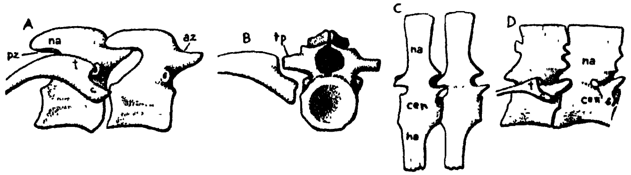


FIG. 95.—The vertebrae of Paleozoic lepospondyls. *A*, *B*, Lateral and anterior views of vertebrae of *Lysorophus; C*, *D*, caudal and dorsal vertebrae of *Crossotelos*, an elongate nectridian. For abbreviations see Figure 94. (*A*, *B* after Sollas; *C*, *D* after Williston.)

Skull.—The skull of primitive labyrinthodonts, such as *Palaeogyrinus* (Fig. 96), is completely roofed by dermal bones; in life these apparently lay close below the surface, barely covered by the skin. The skull pattern is essentially that described for primitive bony fishes, but there have been marked changes in proportions. In the crossopterygian there was a long skull table behind the orbit and "pineal" eye and a relatively short snout. In typical tetrapods the skull table is much shortened, the snout greatly lengthened, with consequent modifications in the development of the bones concerned.

The rather variable fish pattern has settled down to a fixed set of bones that, with relatively few changes, can be followed throughout the labyrin-

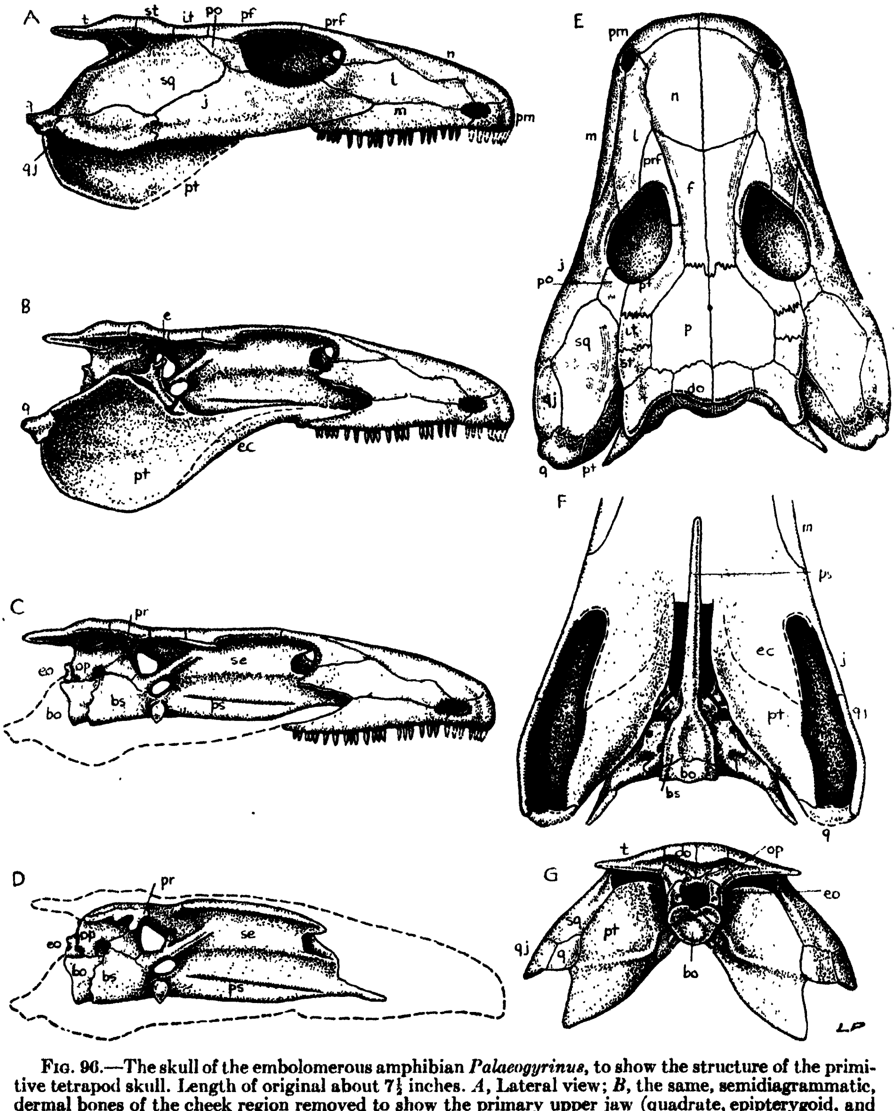


FIG. 96.—The skull of the embolomerous amphibian *Palaeogyrinus*, to show the structure of the primitive tetrapod skull. Length of original about 7½ inches. *A*, Lateral view; *B*, the same, semidiagrammatic, dermal bones of the cheek region removed to show the primary upper jaw (quadrate, epipterygoid, and associated dermal bones—pterygoid and ectopterygoid); *C*, the same, primary upper jaw removed; *D*, the braincase (and parasphenoid), skull outlines in dashed line; *E*, dorsal view of skull; *F*, posterior part of palate; *G*, occiput. (*A*, *D–G* after Watson; *B* and *C* reconstructed from his data.) Lateral-line canals stippled. Abbreviations for this and other amphibian and reptilian skulls: *a*, angular; *ar*, articular; *bo*, basioccipital; *bs*, basisphenoid; *c*, coronoid; *d*, dentary; *do*, postparietal (dermal supraoccipital); *e*, epipterygoid; *ec*, ectopterygoid; *en*, external nares; *eo*, exoccipital; *f*, frontal; *fm*, foramen magnum; *in*, internal nares; *ina*, internasal; *it*, intertemporal; *j*, jugal; *l*, lacrimal; *m*, maxilla; *n*, nasal; *on*, otic notch; *op*, opisthotic; *or*, orbit; *p*, parietal; *pa*, prearticular; *pap*, palpebral; *pd*, predentary; *pf*, postfrontal; *pl*, palatine; *pm*, premaxilla; *po*, postorbital; *pop*, preopercular; *pos*, postsplenial; *pp*, postparietal; *pr*, proötic; *prf*, prefrontal; *ps*, parasphenoid; *pt*, pterygoid; *pv*, vomer (prevomer); *q*, quadrate; *qj*, quadratojugal; *r*, rostral; *s*, stapes; *sa*, surangular; *se* sphenethmoid; *sm*, septomaxillary; *so*, supraorbital; *soc*, supraoccipital; *sp*, splenial; *sq*, squamosal; *st*, supratemporal; *t*, tabular; *v*, vomer.

thodonts and the higher, amniote classes. Nasal and frontal elements, small and often difficult to identify in crossopterygians, are prominent and elongate structures. The parietals, inclosing the pineal opening, are relatively short and placed far back on the skull. There are well-developed premaxillae and maxillae. A circumorbital series includes five bones: prefrontal, postfrontal, postorbital, jugal, and lacrimal. The last sometimes extends all the way from orbit to nostril and comes to carry the tear duct (a fish eye is naturally bathed in water, but that of a land form must be kept moist and have a duct to carry off superfluous liquid). There is a single external nasal opening, or naris, typically bounded by premaxilla, maxilla, nasal, and lacrimal; in primitive types a small element—the septomaxilla—forms part of the margin of the opening and may exclude the lacrimal. A large squamosal and a quadratojugal are present on the cheek, both having a contact with the quadrate bone at the jaw articulation. At the side of the parietal lie one or two temporal elements—a supratemporal and an intertemporal, the latter frequently absent. At the back of the roof are postparietals (dermal supraoccipitals), much reduced in extent from the condition seen in crossopterygians, and, at the corners of the skull table, tabulars.

With the loss of the gills the operculum which covered them has disappeared, breaking the sheet of bones which originally extended unbroken from the skull to the shoulder region. The disappearance of the operculum has converted the slit in which the spiracle lay into an open otic (ear) notch, bounded by the tabular above and the squamosal below.

The palate (Figs. 96, *F;* 97) resembles that of the crossopterygians in its basic plan. The premaxilla and maxilla bear a marginal row of sharp teeth. Inside them lie the vomers, the palatines, and the ectopterygoids, which in primitive types, just as in the crossopterygians, usually carry large labyrinthine teeth and associated pits. The pterygoids are large and stretch back to the quadrates; toward the mid-line, processes from them form a movable articulation with the braincase. In the primary upper jaws there ossify only the quadrate and a small epipterygoid farther forward above the pterygoid. The front end of the braincase is bounded below by a slim parasphenoid, between which and the pterygoids are small openings—the interpterygoid vacuities. The internal opening of the nostril (choana) is between premaxilla, maxilla, vomer, and palatine.

The braincase is well ossified. It is, in contrast to that of typical crossopterygians, a fused single structure in which few sutures are visible. At the back may be present four occipital elements—the median basioccipital and supraoccipital and the paired exoccipitals. A single rounded surface mainly on the basioccipital—the occipital condyle—joins the skull with the first vertebra in primitive amphibians and reptiles. In typical crossopterygians a large notochordal canal ran forward from this point through the floor of the braincase. This is absent in amphibians, although there may be a deep pit for the notochord in the center of the condyle. At the sides the opisthotic (paroccipital) extends upward to the tabulars; in front of this is the proötic, the two inclosing the inner-ear region. Ventrally in front of the basioccipital lies a well-developed basisphenoid, which articulates with the pterygoids laterally and is covered below by a dermal element—the parasphenoid. The most anterior braincase element is a tubular ossification—the sphenethmoid; in contrast with crossopterygians, the nasal capsules at the front end of the braincase fail to ossify.

The lower jaw of the labyrinthodonts (Fig. 97) resembles that of the crossopterygians. On the outer surface lies the long dentary, and below this a row of dermal elements including two splenials, angular and surangular. On the inner side within the dentary are coronoids (primitively, three in number) usually bearing an inner series of teeth. There is a long prearticular; and, as in most fish, the primary jaw is represented only by the small articular.

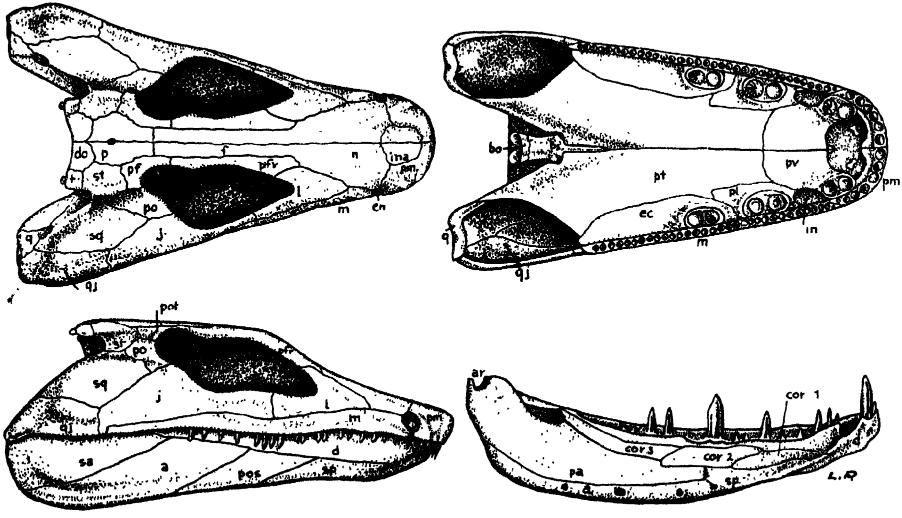


FIG. 97.—The skull of the Carboniferous amphibian *Megalocephalus* [*Orthosaurus*], dorsal, ventral, and lateral views and inner view of jaw; length of original about 12 inches. Lateral-line canals stippled. *pfr*, Prefrontal; *pof*, postfrontal. For other abbreviations see Figure 96. (After Watson.)

With the loss of gill breathing in the adult, the gill arches naturally are reduced, although these elements are still well developed in many amphibians. In higher types there is much further reduction, although even in mammals the cartilages of the tongue and throat are remnants of this skeletal system. They are, however, seldom found in fossils and need little further consideration. The fate of the hyomandibular is discussed below.

Limb girdles.—The skeleton of the limbs and girdles is naturally highly developed. The shoulder girdle (Fig 98, *A*, *B*) lies close behind the head; but in most tetrapods the original connection with the skull has been lost, for in a land animal independent movements of head and shoulder are a necessity. The cleithrum—the large upper bone of the dermal girdle—is retained in primitive land forms, as is the clavicle; in addition, there is developed a median ventral dermal element, the interclavicle, lying on the under side of the chest between the collar bones. These dermal elements tend to be much smaller than they are in the fishes, while the primary shoulder girdle beneath tends to increase in size, since there had been a great increase in the musculature passing from it to the limb. The upper portion of the primary girdle is a flat, scapular blade, below which is an articular surface for the humerus—the glenoid cavity. Ventrally there is a large, flat coracoid plate turning in toward the mid-line of the under side of the body. Primitively, the primary girdle appears to have included but a single ossification—the scapula. In later types (seldom in amphibians) one or two additional coracoid ossifications are developed.

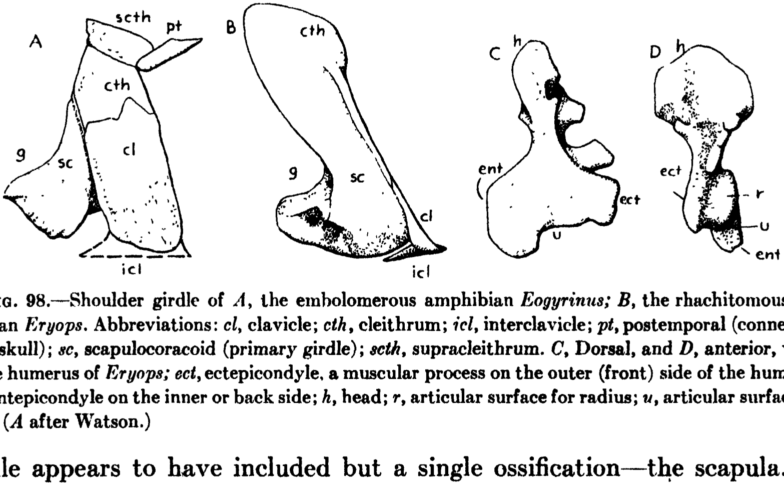


FIG. 98.—Shoulder girdle of *A*, the embolomerous amphibian *Eogyrinus; B*, the rhachitomous amphibian *Eryops*. Abbreviations: *cl*, clavicle; *cth*, cleithrum; *icl*, interclavicle; *pt*, postemporal (connecting with skull); *sc*, scapulocoracoid (primary girdle); *scth*, supracleithrum. *C*, Dorsal, and *D*, anterior, views of the humerus of *Eryops; ect*, ectepicondyle, a muscular process on the outer (front) side of the humerus; *ent*, entepicondyle on the inner or back side; *h*, head; *r*, articular surface for radius; *u*, articular surface for ulna. (*A* after Watson.)

The pelvic girdle (Fig. 99) is a far larger structure than the small plate present in fishes. It has been enlarged to accommodate more muscles; and, while the fish plate is confined to the ventral side of the body, the primitive tetrapod girdle extends far dorsally and is usually joined to the backbone by one or more specialized sacral ribs. This extension is a functional necessity for land dwellers; for the hind legs in a primitive tetrapod must not only support much of the weight but must also give much of the push that propels the body forward. The dorsal extension of the girdle is usually a separate ossification, the ilium. The head of the limb rests in a cavity known as the acetabulum. Below this is a broad ventral plate which joins its fellow of the opposite side in a median symphysis; this plate consists of two ossifications, the pubis (containing a nerve foramen) in front and the ischium behind; the former is often unossified in amphibians.

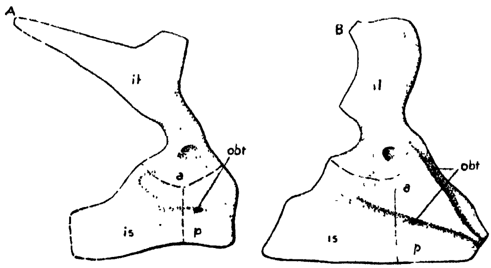


FIG. 99.—Pelvic girdles of *A*, a primitive labyrinthodont (*? Baphetes*), and the rhachitome *Eryops*. Abbreviations: *a*, acetabulum; *il*, ilium; *is*, ischium; *obt*, obturator foramen in pubis; *p*, pubis. (*A* after Watson.)

Limbs.—The limb skeleton is, of course, large in comparison with that of the paired fins of fishes. In the pectoral limb (Fig. 100, *B*) the first segment is a broad and powerful element, the humerus (Fig. 98, *C*, *D*). Its head fits into the glenoid cavity of the shoulder girdle; distally it articulates with two elements which form the second segment of the limb—the radius and the ulna. The former lies on the inner side of the forearm and rests directly under the humerus, supporting much of the weight. The ulna lies outside and usually has a head, the olecranon ("funny bone"), extending above the edge of the humerus; muscles pulling on this open out the arm.

The radius and ulna articulate below with a complex of small elements which constitute the carpus, or wrist (Fig. 101, *A*). Typically there is a proximal row of three elements, the radiale lying under the radius, the ulnare beneath the ulna, and an intermedium lying between the two. Below the last is a large central element (which may articulate directly with the radius), followed by a row of three smaller centralia lying toward the radial side and, finally, a series of five distal carpals, each of which lies opposite the head of a toe.

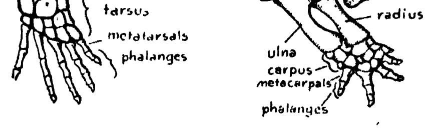


FIG. 100.—*A*, Lateral view of the pelvic girdle and limb of a primitive labyrinthodont (composite); *B*, lateral view of the pectoral girdle and limb of *Eryops*. (After Miner.)

The toes, or digits, of land forms consist of a first segment—a metacarpal —lying within the palm region of the front foot, and beyond this a variable number of elements—phalanges—making up the joints of the free portion of the toe. Five toes are present in the front foot in *Diplovertebron* (Fig. 102, *A*). Most living amphibians and many fossils have but four; there are in some cases, however, traces suggesting that there may have been as many as seven toes originally. The inner digit, corresponding to the human thumb, receives the special name of the pollex. The number of phalanges varies, although the inner toes tend to be shorter than the outer ones. Reptiles typically have a phalangeal formula (counting the number of joints from the pollex out) of 2–3–4–5–3 (or 4); amphibians generally have less.

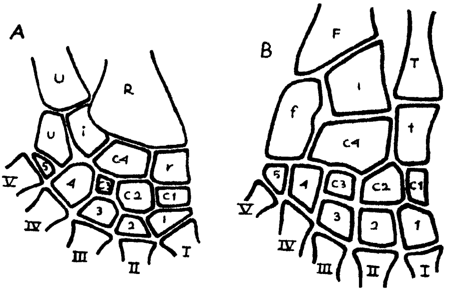


FIG. 101.—Nomenclature of the carpal and tarsal elements. *A*, Diagram of the right carpus of a primitive amphibian; *B*, diagram of the right tarsus. Abbreviations: *I–V*, metacarpals or metatarsals. 1–*5*, distal carpals or tarsals; *c*1–*c*4, centralia. *F*, Fibula; *f*, fibulare; *i*, intermedium. *R*, Radius; *r*, radiale. *T*, Tibia; *t*, tibiale. *U*, Ulna; *u*, ulnare.

The pelvic limb (Fig. 100, *A*) may be compared, part for part, with the pectoral, although a different set of names is used for the bony elements. The femur, usually longer and slimmer than the humerus, constitutes the proximal segment. The next consists of the tibia within and the fibula on the outside. The ankle is the tarsus (Fig. 101, *B*); and the names of the tarsal elements are similar to the carpal ones, except that, of course, the names tibiale and fibulare replace radiale and ulnare; the first toe is the hallux.

The pose of the primitive land limbs (Fig. 100) is quite unlike that found in most living forms, although the straddling walk of a turtle is comparable and, indeed, may have been retained from those early days with comparatively little modification. The proximal segments of the limbs are extended nearly straight out from the body, with the forearm and lower leg extended down at right angles. It is obvious that in such a position only short strides could be taken and that a great deal of the animal's strength was used mere-

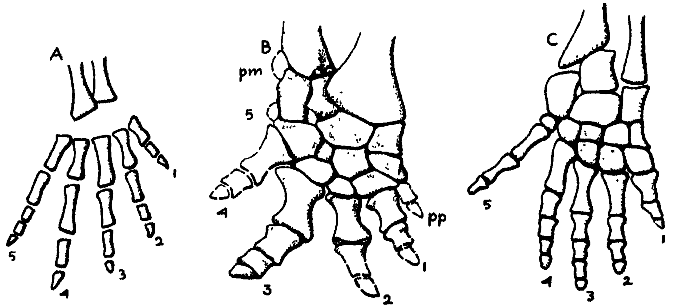


FIG. 102.—The feet of amphibians. *A*, Manus of *Diplovertebron*, a small seymouriamorph; *B*, manus of the rhachitomous amphibian *Eryops*; *C*, pes of the rhachitomous amphibian *Trematops*. Abbreviations: *pm*, postminimus; *pp*, prepollex. (*A* after Watson; *B* after Gregory, Miner, and Noble; *C* after Williston.)

ly in keeping the body off the ground. Walking must have been a slow and difficult process, especially for an animal of any size.

Other organs.—The probable condition of organs of other systems in such a primitive vertebrate may be deduced from conditions still found in living forms. In the adult, gill breathing would have gone and the lungs alone been functional; internal nostrils were, of course, present. Usually in tetrapods all the gill openings except the spiracle disappear. In connection with this change, the circulatory system has been considerably modified; for, instead of passing to the gills, the blood must now pass to the lungs to be purified. This results in the destruction of most of the aortic arches which passed up between the gills. The last one is enlarged and forms part of the passage for blood to the lungs; more anteriorly another persists to carry the blood which has returned from the lungs to the heart, up to the dorsal aorta and so to the body. With this double flow of blood through the heart there is the beginning of a division of this organ into two separate sets of compartments; this division, however, is incomplete in amphibians.

The brain of amphibians is still small, especially the cerebral hemispheres, which are as yet entirely concerned with smell. The sense organs have undergone considerable modifications. The nostrils are adapted for smell under the changed circumstances of air instead of water for a medium. The eyes are usually large; the sclerotic plates, already mentioned as present in many fish groups, were retained in primitive tetrapods. A median eye was present in all early forms but tended to be lost in post-Paleozoic tetrapods of most groups.

The ear region has undergone great change. The balancing function is, of course, retained. Hearing, however, is more difficult in a land type, for air vibrations are so delicate that they cannot effectively set up pulsations which reach the ear through the thickness of the skull. We find in relation to this situation that tetrapods have developed a new mechanism (Fig. 103) which amplifies the vibrations and transmits them to the internal ear. The spiracular opening is retained, but near its outer end it is closed by a thin tight membrane—the ear drum—which picks up the sound vibrations. This drum primitively lies in the otic notch, which corresponds to the spiracular slit of the fish. Attached to the drum is a small bone, the stapes, or stirrup (sometimes termed the columella), which at its inner end abuts on the otic region of the skull. Beneath this inner end there is, in most tetrapods, a foramen (fenestra ovalis) leading into the liquid-filled spaces of the internal ear, so that air waves caught by the drum and transmitted by the stapes set up vibrations in the internal ear; hearing thus results. The stapes is the fish hyomandibular, which was similarly propped up against the otic region of the fish skull. With the tightening of connections between jaws and skull, its old function of a jaw support became superfluous; and, lying in the region just behind the spiracle, it was free to be adapted to this new function.

The lateral-line system of fishes is still retained in the water-living amphibians, and grooves for head canals can often be seen on fossil skulls. Higher in the scale, however, these canals are lost entirely; and even among the amphibians, adult forms which are land dwellers lose them. Their presence or absence in a fossil is a good clue to its habits, for this sensory system is of use only in the water.

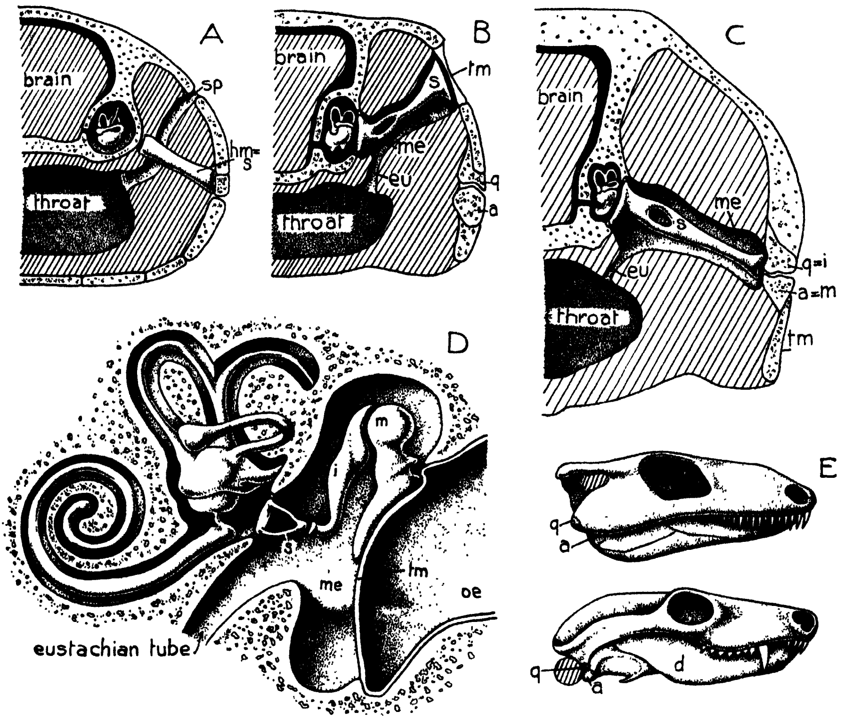


FIG. 103.—*A–D*, A series of stages in the evolution of the ear apparatus. *A*, Cross-section of half of a fish skull in the ear region. The ear structures consist only of the deep-lying sacs and semicircular canals. *B*, An amphibian. The hyomandibular bone (*hm*) of the fish is pressed into service as a sound transmitter, the stapes (*s*); the first gill slit, the spiracle (*sp*), becomes the Eustachian tube (*eu*) and the middle-ear cavity (*me*), while the outer end of the spiracle is closed by the tympanic membrane (*tm*). *C*, A mammal-like reptile. The stapes passes close to two skull bones (*q*, quadrate; *a*, articular) which form the jaw joint. *D*, Man (the ear region only, on a larger scale). The two jaw-joint bones have been pressed into service as accessory ossicles, the malleus (*m*) and the incus (*i*). *E*, A primitive land animal and a mammal-like reptile to show the relation of the eardrum to the jaw joint. At first in a notch high on the side of the skull (the otic notch) occupying the place of the fish spiracle, it shifts in mammal-like reptiles to the jaw region. In mammals the jaw comes to be formed of one bone only (*d*, the dentary), and the bones of the jaw-joint region are freed to act as accessory hearing organs; *oe*, tube of outer ear.

Tetrapod ancestors.—From the description above, it is obvious that among the bony fishes the extinct crossopterygians were the closest to the ancestors of the tetrapods. The lungfish of today are very similar to the amphibians in their embryology and certain soft parts, but this merely indicates the retention of characters present in their crossopterygian ancestors; in such respects as teeth and skull structure the lungfish are definitely on an evolutionary side line and cannot themselves be tetrapod ancestors. As regards the actinopterygians, such features as the absence of internal nostrils and the lack of a large fleshy fin from which a land limb might develop rule this group out of consideration.

In almost every respect the crossopterygians fulfil the requirements for tetrapod ancestors. If a shift in skull proportions be taken into account, the skull-roof patterns in the two groups are readily comparable; the palatal and jaw structures are identical. Even the details of the dentition, with the labyrinthine structure and the peculiar pit and tooth arrangement on the palate, were identical in the two groups. The only obvious difference in cranial structures lies in the fact that the crossopterygian braincase is divided into two sections and that of amphibians is a single unit. It may be that amphibians have descended from unknown crossopterygians in which the braincase joint had not been established. But it is not at all impossible that they have come from typical members of that group and that the fused amphibian braincase is a secondary development. The paired fins of crossopterygians were smaller than those of tetrapods, but the structure of the skeleton of the fins was essentially similar (Fig. 104). In crossopterygians there was a single proximal bone (corresponding to the humerus or femur of tetrapods), two bones in the next segment (as in the forearm or lower leg of land forms), and beyond this an irregular subdivision which is roughly comparable to the foot skeleton of primitive land types. The better-known genera are probably too specialized or too late in time to have been the actual ancestors, but the crossopterygians as a group seem unquestionably to represent the stock from which land vertebrates have sprung.

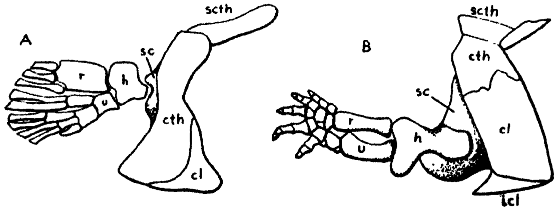


Fig. 104.—*A*, The pectoral girdle and fin of the Devonian crossopterygian *Sauripterus* (after Gregory); *B*, diagrammatic representation of a tetrapod limb placed in a comparable position: Abbreviations: *h*, humerus; *r*, radius; *u*, ulna; for other abbreviations cf. Figure 98.

Origin of tetrapods.—The "why" of tetrapod origin has been often debated. Many of the earliest amphibians appear to have been fairly large forms of carnivorous habits, still spending a large portion of their time in fresh-water pools. Alongside them lived their close relatives, the crossopterygians, similar in food habits and in many structural features and differing markedly only in the lesser development of the paired limbs. Why did the amphibians leave the water? Not to breathe air, for that could be done by merely coming to the surface of the pool. Not because they were driven out in search of food—they were carnivores for whom there was little food on land. Not to escape enemies, for they were among the largest of vertebrates found in the fresh waters from which they came.

Their appearance on land seems to have resulted as an adaptation for remaining in the water.

The earliest-known amphibians lived much the same sort of life as the related contemporary crossopterygians. Both lived normally in the same streams and pools, and both fed on the same fish food. As long as there was plenty of water, the crossopterygian probably was the better off of the two, for he was obviously the better swimmer—legs were in the way. The Devonian, during which land adaptations originated, was seemingly a time of seasonal droughts when life in fresh waters must have been difficult. Even then, if the water merely became stagnant and foul, the crossopterygian could come to the surface and breathe air as well as the amphibian. But if the water dried up altogether, the amphibian had the better of it. The fish, incapable of land locomotion, must stay in the mud and, if the water did not soon return, must die. But the amphibian, with his short and clumsy but effective limbs, could crawl out of the pool and walk overland (probably very slowly and painfully at first) and reach the next pool where water still remained.

Once this process had begun, it is easy to see how a land fauna might eventually have been built up. Instead of seeking water immediately, the amphibian might linger on the banks and devour stranded fish. Some types might gradually take to eating insects (primitive ones resembling cockroaches and dragon flies were already abundant) and, finally, plant food. The larger carnivores might take to eating their smaller amphibian relatives. Thus a true terrestrial fauna might be established.

Amphibian classification.—The problem of the proper classification of the amphibians has been—and still remains—a vexatious one, and no existing system seems particularly satisfactory. We here introduce a different scheme which at the moment appears best to accord with present knowledge of the group (but which may, in turn, become obsolete with increased data regarding amphibian evolution). The two contrasting types of vertebral structures found in amphibians are here regarded as distinctive of two major subdivisions of the Amphibia.

The term Lepospondyli has long been used for a number of fossil groups with the lepospondylous type of vertebral structure; we here use it for a subclass in which we shall include, besides the older groups, the modern orders with a similar vertebral structure—the salamanders, forming the order Urodela, and the wormlike members of the order Apoda.

The second type of vertebra described above—that in which the centra are ossified from blocks or arches of cartilage—is characteristic of a great series of older amphibians known as the Labyrinthodontia and is retained in modified form in the higher amniote classes and, among the Amphibia, in the Anura—the frogs and toads, which appear to be of labyrinthodont ancestry. For this amphibian group is coined the term Apsidospondyli, or forms with arch vertebrae.

This classification is a vertical one, an attempt to distinguish two major lines of descent, each of which includes both older and younger elements. We may note, however, that there has been, since Paleozoic days, a great deal of parallel evolution in both subclasses, so that the modern forms in either case have in common many specialized and degenerate features. For example, in most existing amphibians many of the dermal elements of the skull have disappeared, and the orbital and temporal regions are unprotected by bone. In contrast, almost all Palaeozoic forms of both groups had a completely roofed skull. The term "stegocephalian," referring to this fact, is often used as a designation for the older amphibians. This, however, is inappropriate as a taxonomic term, for it merely distinguishes between geologically older and younger amphibians of various groups without regard to their true relationships.

Labyrinthodonts.—The largest and most important series of early fossil amphibians is that included in the superorder Labyrinthodontia, defined as primitive amphibians with the apsidospondylous type of vertebrae described above. It appears probable that the earliest-known Devonian amphibians were members of the labyrinthodonts, in a broad use of the term; and practically all the larger amphibians of late Paleozoic and Triassic belonged to this group. Some of the more primitive types resembled greatly the oldest reptiles and are unquestionably ancestral to them, and thus to all higher tetrapods. More than that, the earlier representatives of the group are structurally close to the ideal tetrapod ancestor.

The structure of a rather primitive labyrinthodont has been described above in some detail. But the labyrinthodonts were not, so to speak, any more disposed to remain idealized ancestral types than any other group of organisms which are of importance as phylogenetic connecting links. They themselves underwent a very considerable series of evolutionary developments between their first appearance and their extinction in Triassic times. The earliest types were primitively aquatic forms, of which *Eogyrinus* is fairly typical. Even in the Carboniferous, however, there appears to have been a trend toward stouter-limbed land types; from such forms may have sprung the reptiles. But, in the Permian, regression took the place of progress in limbs and other structures, and the Triassic end-forms of the order were degenerate types, incapable of leaving the water.

Many structural trends accompanied this sequence of stages. The body shape was primitively well rounded and rather fishlike; in later types a depressed body and a stumpy tail became common. The skull, at first comparatively high and narrow, tended in later forms to flatten out and become very broad and depressed. A single occipital condyle was present at first; in time this divided into two separate articulations. On the palate the primitively small openings between the pterygoids and the parasphenoid opened out into huge interpterygoid vacuities, and the movable joint between the pterygoids and the braincase became a broad, firm union of these bones. Ossifications in the braincase were much reduced. The limbs tended early to increase in size but in later types dwindled into insignificance. In the shoulder region the clavicles and interclavicle expanded into broad plates on the flat lower surface of the chest. At first, progress and the throwing-off of lines leading to other tetrapod groups; then degeneration into flat, sluggish water types; finally extinction—such seems to have been the history of the labyrinthodonts.

It is difficult to establish good criteria for subdivision of the labyrinthodonts. They will here be considered as constituting five orders: Ichthyostegalia, Rhachitomi, Stereospondyli, Embolomeri, Seymouriamorpha.

The earliest amphibians.—Amphibians are abundant and varied in the Carboniferous, and it is therefore certain that the group originated in the Devonian. Until recently no skeletal remains of amphibians were known from that period, but in the last few years two discoveries have been made which shed light on this earliest chapter in tetrapod history. These discoveries are not, however, too satisfactory; for in one case the find is definitely Devonian but doubtfully amphibian, in the other definitely amphibian but doubtfully Devonian.

In the famous Upper Devonian beds at Scaumenac Bay in Canada there has been found, among the plentiful remains of fishes, a single small and incomplete skull roof of unusual nature, which has been named *Elpistostege* (Fig. 106). As may be seen, the pattern of the bones is comparable, in general, to that of crossopterygian fishes but is even closer to that of the ichthyostegal amphibians discussed below. We have noted that a major difference between crossopterygian and amphibian skulls lies in the relative development of front and back portions; *Elpistostege* is intermediate in its proportions. It thus appears to represent in skull structure a transitional stage between the two groups. We know nothing at all of its postcranial skeleton—whether it bore fins or legs. Perhaps significant in attempting to reach a decision is the fact that the roof shows no trace of the transverse break behind the parietals which in crossopterygians is associated with the bipartite braincase. We may very tentatively assign it to the Amphibia and associate it with the more highly developed ichthyostegids next to be described.

In the Paleozoic deposits of Greenland have been discovered a series of skulls described under the generic names *Ichthyostega* (Fig. 105) and *Ichthyostegopsis.* The fresh-water beds from which they are derived are of somewhat uncertain age; but, if not late Devonian, they are at the least earliest Mississippian; and these genera are the oldest-known forms which can be definitely classed as amphibians. They were animals of fairly good size, for the rather high and narrow skulls are half a foot or so in length. The roof pattern is, in general, highly comparable to that of Carboniferous and Permian labyrinthodonts. It is, however, primitive in a number of respects which are suggestive of the crossopterygian condition. The snout is rather less developed than in most amphibians, and there is present a rostral element comparable to the rostrals of many bony fishes; the skull table is unusually long for an amphibian. There is no evidence of the fish operculum, but there is a remnant of the preopercular bone which in bony fishes connects it with the

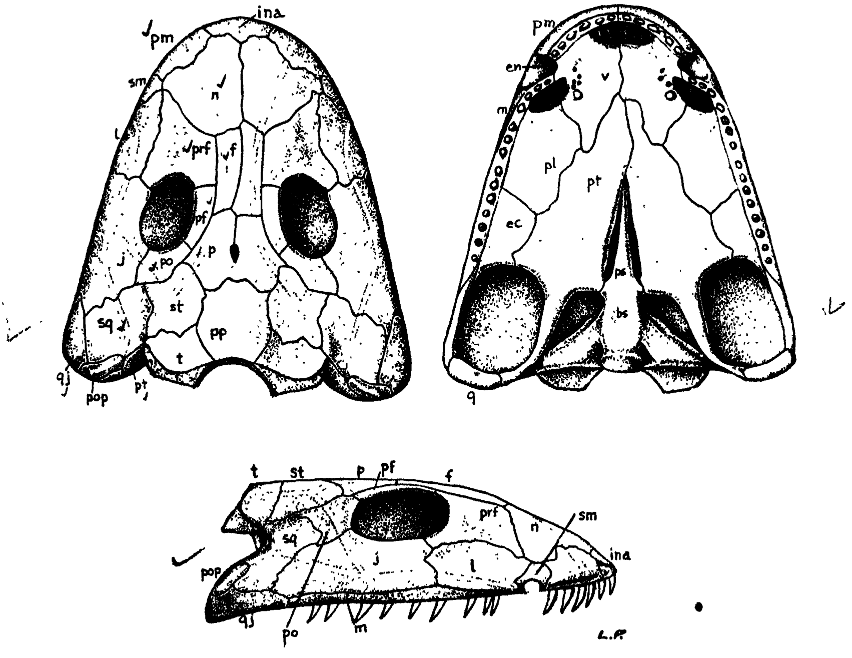


FIG. 105.—Dorsal, ventral, and lateral views of the skull of *Ichthyostega;* length of original about 8 inches. For abbreviations see Figure 96. (After Säve-Soderbergh and Westoll.)

cheek. The snout is so rounded that the nasal openings are invisible in dorsal view. In most land forms the internal and external openings are separated by a broad bar of bone; here they are separated by only a slender process of the maxilla—presumably a primitive condition. The palate is primitive in nature, with small interpterygoid vacuities.

There are a few characters in which *Ichthyostega* shows advances or specializations rather than truly primitive amphibian conditions. In some other early amphibians (embolomeres) the otic notch is deep, and the cheek region below it rather loosely attached to the skull roof, much as in the comparable spiracular region of crossopterygians; in ichthyostegids the notch is shallow and the bones about it solidly fused. Other early groups of labyrinthodonts have an intertemporal bone in the skull roof; this is absent in *Ichthyostega*. We may conclude that the ichthyostegids, despite their antiquity, are not the generalized ancestors of other amphibian groups but, rather, a very early offshoot from this ancestral stock.

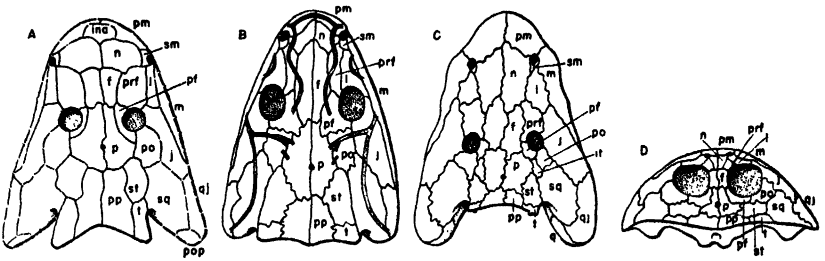


FIG. 106.—The skull roof of various labyrinthodonts: *A*, the primitive *Elpistostege* of the Upper Devonian (×$\frac{1}{5}$ approx.), the lateral portions restored; *B*, *Colosteus*, a Pennsylvanian ichthyostegan (×$\frac{1}{4}$ approx.); *C*, *Edops*, a primitive Permo-Carboniferous rhachitome (×$\frac{1}{20}$ approx.); *D*, *Gerrothorax*, a Triassic short-skulled stereospondyl (×$\frac{1}{10}$ approx.); *i*, intertemporal. For other abbreviations see Figure 96. (*A* after Westoll; *D* after Fraas and von Huene.)

There are no data as to the postcranial skeleton in *Ichthyostega*. However, this group of amphibians, which may be called the order Ichthyostegalia, persisted into the Carboniferous and is last represented in the Pennsylvanian by *Colosteus* (Fig. 106) and *Erpetosaurus* (Fig. 107). Here the postcranial skeleton is of the general type seen in other early labyrinthodonts. The vertebrae, although incompletely known, appear to have a primitive structure of the general rhachitomous type, and we are justified, therefore, in including the Ichthyostegalia among the labyrinthodonts.

It is of interest that these late members of the group parallel other labyrinthodonts in some of the degenerate and specialized trends discussed in the last section. For example, *Ichthyostega* had small interpterygoid vacuities; in *Erpetosaurus* (Fig. 107) they are large and rounded, as in various other amphibian groups of the late Carboniferous and Permian.

Embolomeres.—A very different but also very primitive group of labyrinthodonts is that of the order Embolomeri. Diagnostic is the vertebral structure (Fig. 94), in which both intercentra and pleurocentra have become complete disks. They are exceedingly primitive in many respects; and, on the other hand, they show features suggestive of relationship to the reptiles. The embolomeres, in genera such as *Eogyrinus* (Fig. 108) and *Palaeogyrinus* (Fig. 96), appear to have been common large amphibians of the Carboniferous; they became extinct, however, at the beginning of Permian times. Our foregoing account of primitive amphibian structure was based in great measure on such embolomeres. The skull, as expected in primitive forms, was relatively high and narrow and sometimes elongated; there was but a single occipital condyle. The skull-roof pattern was of a very primitive type. There was a deep otic notch; the cheek plate below it appears to have been but loosely attached to the skull roof. Both intertemporal and supratemporal elements are present in the skull table, and a further point of distinction from ichthyostegids in this region is the fact that the tabular is relatively large and is in broad contact with the parietal. The palate is primitive in nature, with small vacuities, and, as in bony fishes, there is a movable articulation between braincase and palate on either side. The braincase is very well ossified. In the only forms in which the skeleton is at all well known, the body was much elongated, with a powerful tail but small limbs. Such embolomeres were, we believe, persistent, water-dwelling fish-eaters. There is evidence suggesting that the limb girdles were of a primitive and rather fish-like nature. There appears to have been but a loose connection between pelvic girdle and backbone; in some embolomeres, as in bony fishes, the dermal shoulder girdle may have still connected with the head, a projecting "horn" on the tabular bone forming the point of attachment.

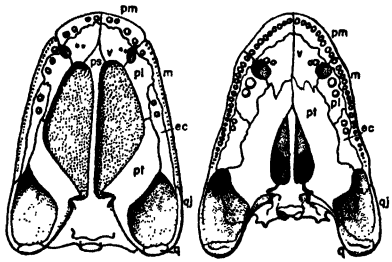


FIG. 107.—*Left*, palate of the Pennsylvanian ichthyostegan *Erpetosaurus* (×½ approx.). (After Steen and Romer.) *Right*, palate of *Edops* (×$\frac{1}{20}$ approx.). For abbreviations see Figure 96.

In many skeletal features the embolomeres are archaic types and have been regarded as representatives of the stem amphibian stock. The vertebral structure, however, is not that which one would expect in ancestral forms, and there are features of the skull pattern which suggest that they had specialized to some extent toward the reptiles. They were, however, an important group of persistently primitive amphibians and played a major part in the life of the Coal Measures swamps and pools.

Diplovertebron (Figs. 102, 109) is of interest as a link between the embolomeres, on the one hand, and the seymourians (next to be described) and reptiles, on the other. This is a small amphibian from the late Pennsylvanian of Europe. The skull is exactly comparable with that of embolomeres, and the vertebrae are usually described as embolomerous in nature. However, the intercentra appear not to be complete disks but large crescents, incomplete above, suggesting a connection with *Seymouria* and the reptiles; also suggestive of such relationships is the five-toed manus and the long-stemmed interclavicle.

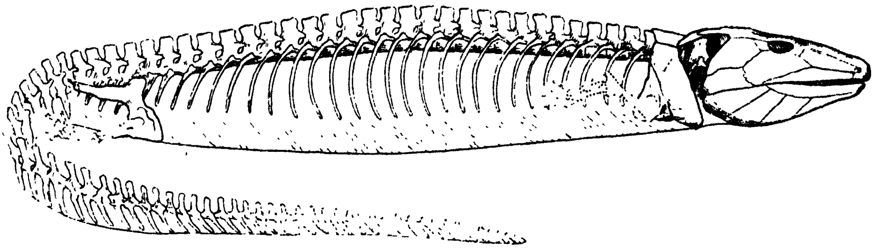


FIG. 108.—*Eogyrinus*, a Carboniferous embolomerous amphibian; estimated length about 15 feet. (After Gregory, modified from Watson.)

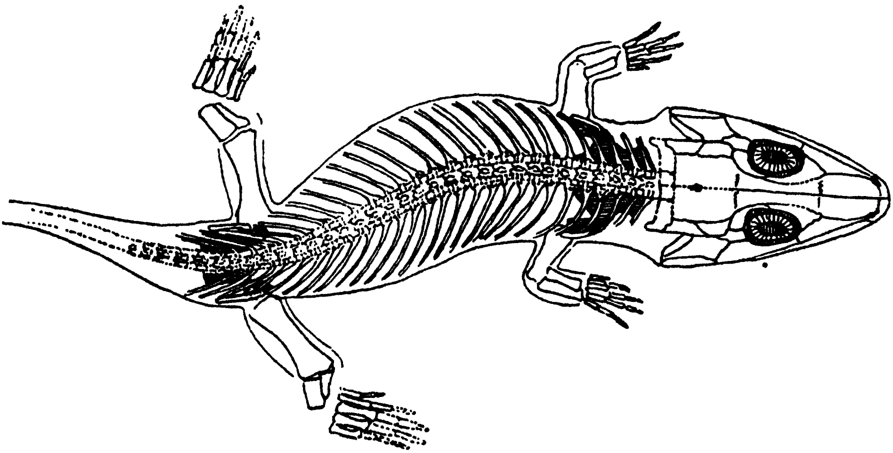


FIG. 109.—Dorsal view of the skeleton of *Diplovertebron*, a small seymouriamorph amphibian from the late Pennsylvanian of Bohemia. (From Watson.)

Seymouriamorpha.—*Seymouria* (Figs. 110, 111), a form of modest size from the Lower Permian red beds of Texas, is one of the most frequently discussed of early tetrapods, for it exhibits such a combination of amphibian and reptilian characters that its proper position in the classification of vertebrates is an unsolved problem. Many of its structural features are those common in the skeletons of a wide variety of early tetrapods—amphibians and reptiles alike. The skull roof is identical in pattern with that of the embolomeres, even to the presence of an intertemporal bone, not present in reptiles. The palate is likewise primitive; there are even persistent palatal tusks of amphibian type on vomers and palatines. There is a single occipital condyle, as in primitive members of both classes, and the braincase shows features of both groups. The limbs and girdles show many characters common to all primitive tetrapods. There are a number of features comparable to those in reptiles rather than to typical amphibians. The humerus is pierced by a foramen found in primitive reptiles but not in typical amphibians; the interclavicle has a long stem, whereas that of typical amphibians is short and broad; the manus is five-toed; the phalangeal formula is 2–3–4–5–3(4); the shoulder, as in reptiles but not in typical amphibians, has a ventral coracoid ossification in addition to the scapula. But the humeral foramen is found in embolomeres, the stemmed interclavicle in *Diplovertebron;* this last form has a five-toed manus, although with a lower phalangeal count. The ilium, usually slender in amphibians, is expanded, as in reptiles generally. Reptiles commonly have two or more sacral ribs; amphibians, one; *Seymouria* appears to be in process of incorporating a second rib. The vertebrae (Fig. 94) are like those of primitive reptiles (cotylosaurs) in their broad and swollen neural arches and in the structure of the central region, with a complete disk of true

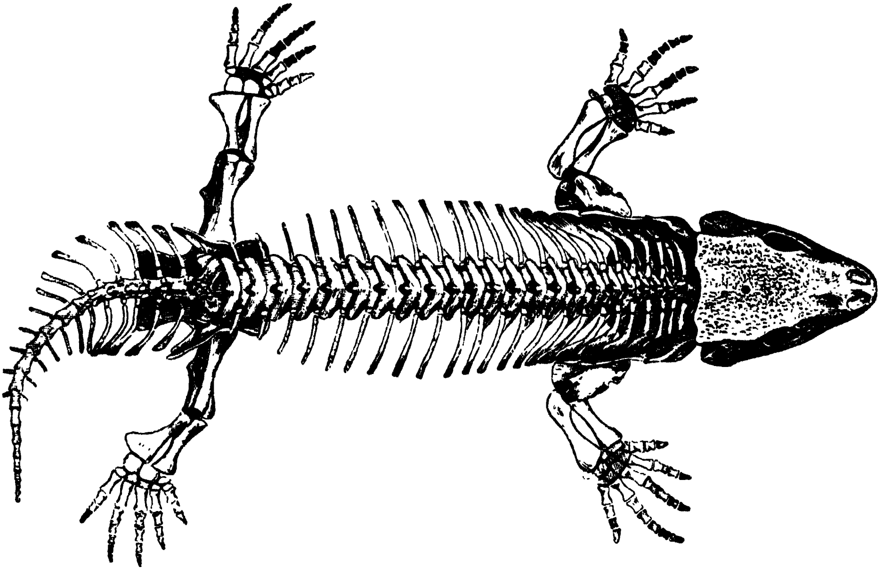


Fig. 110.—*Seymouria* in dorsal view; original about 20 inches long. (From Williston.)

centrum and a wedge-shaped intercentrum; but the intercentrum is unusually large, and we have noted a similar build in *Diplovertebron.*

Seymouria thus seems to stand almost exactly on the dividing line between amphibians and reptiles; we have here a demonstration of the fact that there is no clear-cut distinction between the two classes in skeletal structures. The distinction between them is fundamentally one of modes of development. Did *Seymouria* lay its eggs, frog-fashion, in the water or produce shelled, land-laid eggs of amniote type? Probably this question will never be answered.

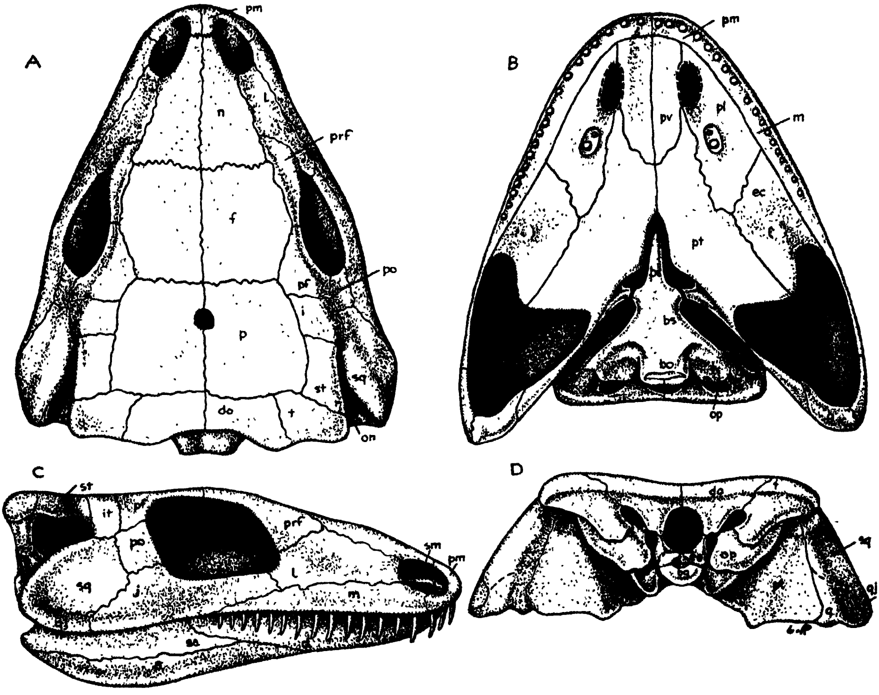


FIG. 111.—The skull of *Seymouria*. *A*, Dorsal; *B*, ventral; *C*, lateral; and *D*, posterior views. Length of original about 4½ inches. For abbreviations see Figure 96. (After Williston and White.)

An indirect answer, however, seems to be supplied by a consideration of *Kotlassia* (Fig. 112). This is a small amphibian from the Upper Permian of Russia, which seems to be a late surviving relative of *Seymouria.* It shows many features comparable to those found in *Seymouria;* it is, however, much more like typical amphibians than is that genus. In its flattened skull, the relatively feeble ossification of the skeleton, and other features, it appears to be undergoing a series of regressive changes associated in typical amphibians with a reversion to permanent water-dwelling existence. This evolutionary parallelism strongly suggests that *Seymouria* and its kin, although close morphologically, and perhaps phylogenetically, to the reptiles, were still on the amphibian side of the boundary and should be included, as the order Seymouriamorpha, with their labyrinthodont relatives.

The Rhachitomi.—Returning from this excursion into the neighborhood of the Reptilia, we may now consider the most abundant and typical of all labyrinthodont groups, the Rhachitomi. This order includes nearly all of the larger amphibians of the Permian period; but, as will be seen, there is evidence indicating that the group had originated at a much earlier time and had had a long independent history. The characteristic Permian forms occupy a middle position in the series of regressive stages noted in the labyrinthodonts; but it will be seen that there appear to have been ancestral rhachitomous types of much more primitive nature.

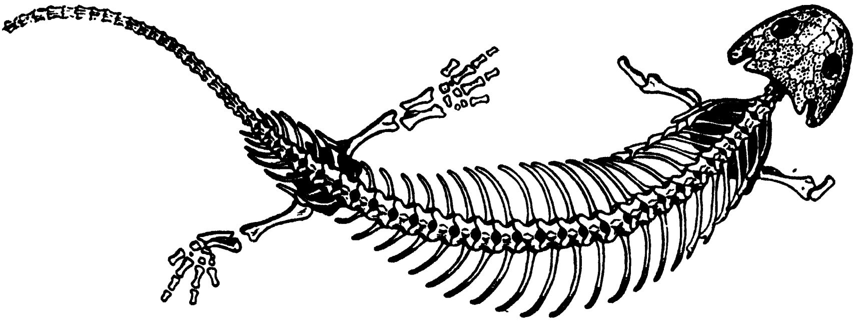


FIG. 112.—The skeleton of the Upper Permian seymouriamorph *Kotlassia*, about $\frac{1}{8}$ natural size. The manus is unknown. (From Bystrow.)

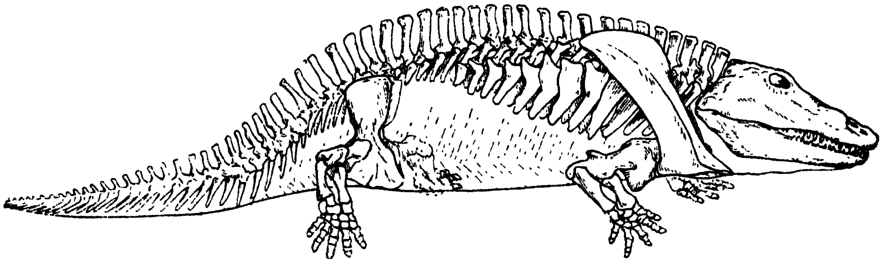


FIG. 113.—*Eryops*, a large Lower Permian rhachitomous amphibian about 5 feet in length. (From Gregory.)

The group name is derived from the rhachitomous structure of the vertebrae (Fig. 94). Apparently, they share this feature and certain others with the ichthyostegids, but the rhachitomes are probably not derived from those early types and can be readily distinguished from them.

A typical Permian form is *Eryops* (Figs. 113, 114) of the Lower Permian of Texas; *Actinodon* is a very similar European animal of the same age. The limbs in *Eryops* were powerful, although short; and such a type presumably spent much of its life on land, although it probably kept near the water.

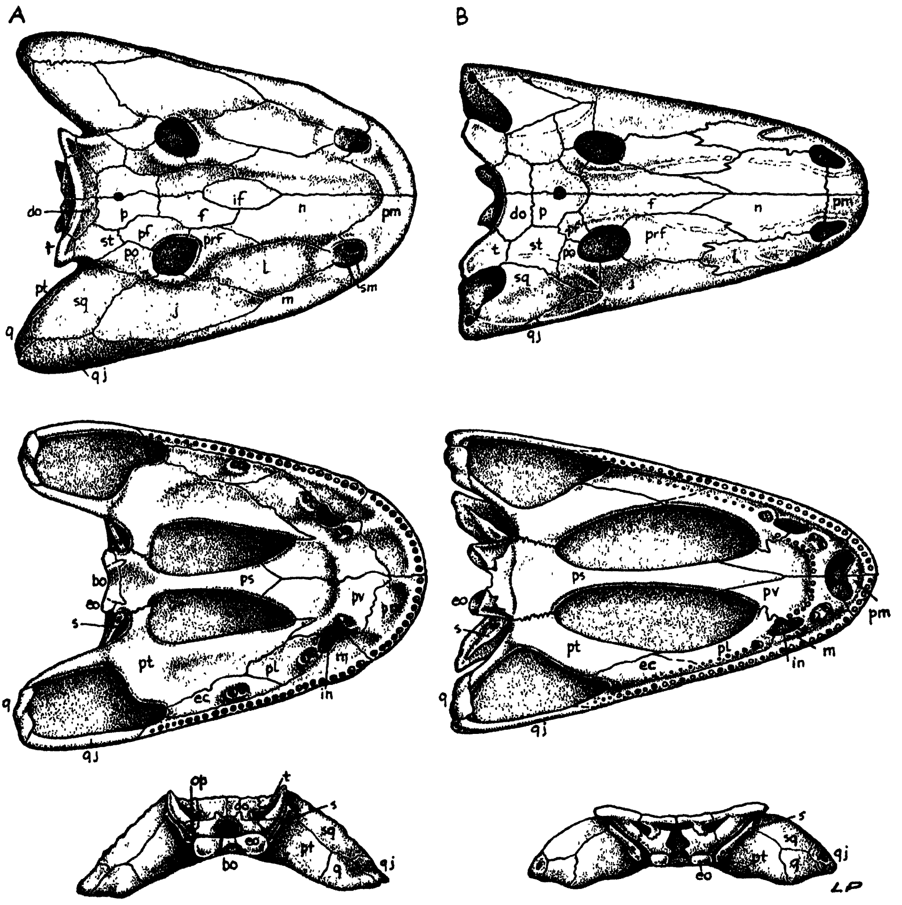


FIG. 114.—The skulls of *A*, the rhachitomous labyrinthodont *Eryops* and *B*, the stereospondyl *Capitosaurus*—dorsal, ventral, and occipital views. *if*, Interfrontal. For other abbreviations see Figure 96. (*Eryops* mainly after Broom, Watson, and Williston, length about 18 inches; *Capitosaurus* after Schroeder and Watson, length about 12 inches.)

There were only four well-developed fingers in the front foot (Fig. 102, *B*), as is the case in all remaining amphibians, although there were still indications of a former higher number. The skull was slightly degenerate, for it was somewhat depressed; and the condyle was tending toward a double condition, since the basioccipital which formed its central part was small. The interpterygoid vacuities were considerably enlarged, and the pterygoids were now firmly attached to the broad parasphenoid which stretched back over the reduced basisphenoid.

The skull-roof pattern shows details diagnostic of the Rhachitomi. As in ichthyostegids and in contrast to embolomeres, the otic notch is rounded, with the cheek solidly united with the skull roof in front of the notch, and the tabular is relatively small and without a contact with the parietal. Such features suggest a relationship between the two groups, but the relationship is, at best, a distant one. The fact that *Eryops*, like the ichthyostegids, lacks an intertemporal bone appears to be a further point of similarity. But this is not the case; as will be seen, early rhachitomes, like embolomeres, had retained this element.

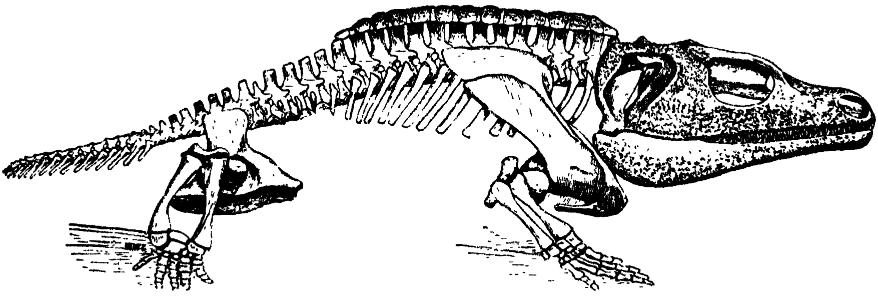


FIG. 115.—*Cacops*, a small rhachitomous amphibian from the Lower Permian. Original about 16 inches long. (From Williston.)

There were numerous side branches of the rhachitomous stock in the Permian. An interesting type is that shown in *Cacops* (Fig. 115) and its allies. These forms were the most terrestrial in habits of the Rhachitomi, with well-developed legs and a much-reduced tail. Presumably as a defense against carnivorous reptiles (already abundant in the Lower Permian), dermal armor plates were present on the back above the neural spines. This is an early instance of the development of armor in land animals; we shall find similar structures again and again in reptilian groups and in certain mammals as well. The otic notch of some of these forms was inclosed behind, giving a complete ring of bone around the ear drum.

Even among the Permian Rhachitomi many forms were already degenerating, slumping back into the water, with very depressed skulls and much reduced limbs. *Trimerorhachis* was a typical form of this sort, which structurally led to the final stage in labyrinthodont evolution.

We may here note the history of the "branchiosaurs" (Figs. 116, 117). In the late Pennsylvanian and early Permian deposits of Europe there have been found many skeletons of tiny amphibians which show a number of points of resemblance to the rhachitomes but differ not only in their small size but in a much less ossified skeleton, a shorter skull, and other features. In many specimens clear traces of gills were present, and hence the name *Branchiosaurus* was appropriately given them. The vertebrae were feebly ossified and poorly preserved and were thought to differ from those of the Rhachitomi; on this account the branchiosaurs were considered to represent a separate order, the "Phyllospondyli"; and a number of other Paleozoic amphibians were provisionally included in this group.

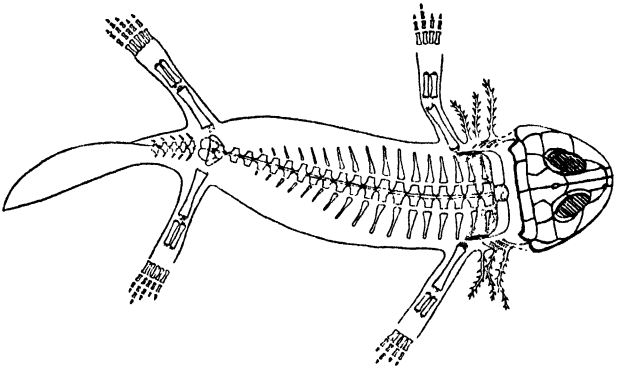


FIG. 116.—The skeleton of "*Branchiosaurus*," a larval rhachitomic from the Lower Permian, with remains of both external and internal gills. (After Bullman and Whittard.)

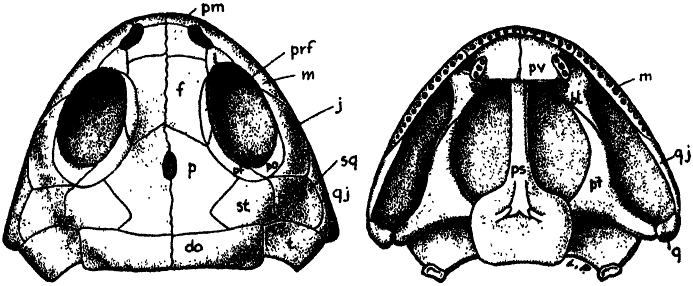


FIG. 117.—Skull of "*Branchiosaurus*," dorsal and ventral views, enlarged. For abbreviations see Figure 96. (After Bullman and Whittard.)

A study of growth stages, with changing proportions and increasing ossification in larger specimens, seems to show, however, that the branchiosaurs are merely larval labyrinthodonts, many of them gradually transforming, with increase in size, better ossification, and loss of gills, into rhachitomes of the *Eryops* type. The "order Phyllospondyli," long included in every account of the Amphibia, is thus a purely imaginary group.

We have earlier noted a series of stages in structural degeneration through which the labyrinthodonts tended to pass in the late Paleozoic and Triassic. The Permian rhachitomes exhibit an intermediate stage in this process, the Carboniferous embolomeres a more primitive one. It has been held that the rhachitomes, therefore, were descended from embolomeres. This, however, is probably not the true situation. In recent years evidence has been gained which indicates that the rhachitomes were a far older group than we had once thought and include within their own membership types of very primitive structure. Recently there have been discovered and identified as rhachitomes various Pennsylvanian forms, large and small, such as *Edops* (Figs. 106, 107) and *Dendrerpeton,* which show a host of primitive features: the skull is relatively higher than in *Eryops;* the palatal vacuities are relatively small; the articulation of braincase and palate is movable in primitive fashion; there is a single skull condyle instead of the double condition seen in *Eryops;* and an intertemporal bone is present on the skull roof.

We have not as yet identified rhachitomes positively in the Mississippian, but in that period the commonest amphibians were forms of the type of *Loxomma* and *Megalocephalus* [*Orthosaurus*] (Fig. 97). The loxommids possessed one obvious but superficial specialization—a long forward extension of the orbit, which may have lodged a gland of some sort. Apart from this, they were very primitive amphibians indeed in every skull feature, and in details of skull pattern they show a close resemblance to the rhachitomes of later days. Their vertebrae are unknown, but it is likely that they are an early offshoot of the rhachitomous stock. It is not too improbable that we shall one day be able to carry the story of the rhachitomes back to ancestral amphibians of the Devonian.

Stereospondyls.—In the order Stereospondyli are included the last and most degenerate members of the Labyrinthodontia. The diagnostic feature lies in the vertebral construction (Fig. 94). The pleurocentra have disappeared completely, and the whole central region is formed by the intercentra, which have grown from ventral crescents to nearly complete disks, notched, however, at the top for the notochord. The head was large, the body and tail short, and the limbs were tiny and obviously inadequate to support the body on land. The trunk was very broad and flat, and the interclavicle and clavicles formed a broad chest plate upon which the animals presumably rested. The skull (Fig. 114), too, was much flattened, and the eyes (as in all bottom-living forms) looked directly upward. The ossifications in the braincase had almost entirely disappeared, save the exoccipitals which formed the two distinct condyles. Beneath, the huge parasphenoid covered the entire braincase area, and there was a broad immovable connection between this bone and the pterygoids. The interpterygoid vacuities were very large.

The stereospondyls are clearly of rhachitome derivation, and Upper Permian and very early Triassic deposits contain transitional genera. The stereospondyls are common in numerous Triassic beds in almost every region of the world. A maximum in size was reached by the appropriately named *Mastodonsaurus*, with a skull over a yard in length. In many forms, such as *Capitosaurus*, the skull was of "orthodox" outline, with the orbits rather toward the back of the skull and the facial region moderately long. In *Trematosaurus* and its relatives the snout was excessively long. These last forms were fish-eating types; evidence from Spitzbergen indicates that some of them were actually marine in habitat, a situation unparalleled among other amphibians, for salt water is fatal to larval forms.

Buettneria (Fig. 118) is typical of a group common in the North American Triassic, in which the orbits were near the front of the long skull. Still another variant is present in *Brachyops* and its allies (Fig. 106), in which the skull is very short and broad.

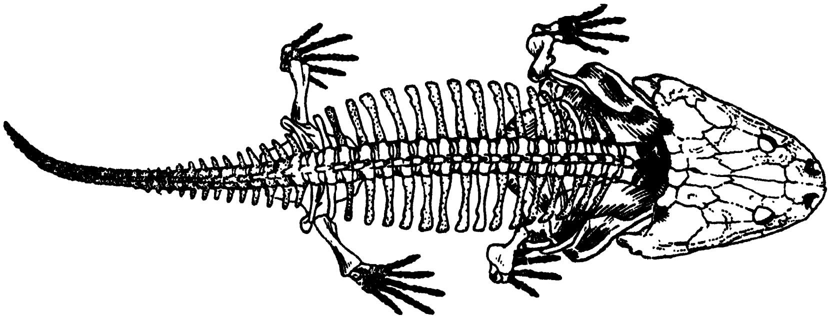


FIG. 118.—Dorsal view of the skeleton of the Triassic stereospondyl *Buettneria*, $\frac{1}{20}$ natural size (From Sawin.)

Despite their abundance, the stereospondyls did not survive the Triassic. Their extinction is perhaps to be correlated with the fact that at that time there were developing numerous reptilian types of similar aquatic habits with which the more lowly organized amphibians could not successfully compete.

The evolution of frogs.—Far different in almost every respect from the labyrinthodonts are the modern frogs and toads of the superorder Salientia, which we shall here regard as constituting, with certain fossil relatives, an order Anura. These modern amphibians are very degenerate and specialized types.

Some of their degenerate features are shared with the urodeles, although the two have evolved from very different Paleozoic stocks. The skull in both groups is much flattened, and there has been much reduction in ossification of the braincase. Exoccipitals bearing the paired condyles and a sphenethmoid are almost universally present, and there is usually an opisthotic; but other braincase elements, such as basioccipital, supraoccipital, and basisphenoid, are practically unknown. The pineal opening is lost, and many roofing bones have disappeared; the skull is no longer solidly roofed. Almost without exception every bone of the circumorbital series has vanished, together with the temporal elements, tabulars, and dermal supraoccipitals, leaving of the dermal bones only a reduced central row and a lateral rim along the jaw. As in the late members of the older groups, there are in the palates of frogs and salamanders large interpterygoid vacuities separated by an expanded parasphenoid. Both ectopterygoids and epipterygoids disappear, and the other elements may be much modified; the pterygoids are immovably attached to the braincase. The jaw elements are much reduced; at the most, we find a dentary, angular, prearticular, articular, and a single coronoid, as compared with the ten bones present in early labyrinthodonts; and there may be still further reduction.

There is much loss of ossification in the limb skeleton; the pubis is never ossified, and the carpus and tarsus may remain largely formed of cartilage. There are never more than four typical digits in the front foot. There is no trace of scales in either frogs or salamanders.

Beyond these features possessed in common with salamanders, the frogs show numerous peculiar specializations. Most obvious are the absence of a tail and the extremely long, hopping hind legs, in which an extra joint has been formed from elongated tarsal elements. The internal structures are also highly modified. The vertebrae lack true centra in most cases; the neural arches grow down around the notochord and form the body of the vertebrae, although in some primitive genera small nubbins along the ventral margins represent vestigial intercentra and pleurocentra. There are often only six or eight vertebrae in the entire backbone, although at the posterior end of the column, beyond the sacrum, there is a peculiar long spike of bone which appears to represent a dozen or so tail vertebrae fused into a solid mass. The ribs have almost universally disappeared and are replaced by long transverse processes.

The ilium is extended into a long rod which reaches forward a considerable distance to connect with the last of the vertebrae. The hind legs are very long and powerfully developed for jumping, and tibia and fibula are fused into a single element, as are the radius and ulna in the front leg. The shoulder girdle retains all the primitive parts, although it is rather peculiar in form and seemingly strengthened to take up the jars caused by the hopping gait. There is even a separate coracoid ossification, an unusual feature in amphibians. Alone among living tetrapods, the frogs apparently have a vestige of the cleithrum in a partially ossified area above the scapula proper.

The frogs are the most successful of modern amphibians. Their history can be readily followed back to the Jurassic. The remains from that period, although fragmentary, indicate that the frogs were already modern in build; and until recently their earlier history was unknown.

Two recent discoveries offer a solution to this problem of frog ancestry. A nodule from the early Triassic of Madagascar contains the skeleton of a small amphibian which has been named *Protobatrachus*. The specimen displays a skull which is very similar to that of modern frogs and toads. The postcranial skeleton, on the contrary, is not particularly froglike except for elongation of the ilium. The trunk is moderately long; the tail not shortened; ribs were present; the limbs, while moderately long and slender, show none of the hopping specializations seen in the modern types. Apparently skull specialization preceded trunk and limb specialization in anuran evolution.

A second recent study appears to carry the frog story back to the Pennsylvanian in time and back to the labyrinthodonts in phylogeny. *Amphibamus* and *Miobatrachus* (Figs. 119, 94), rare amphibians of very small size from the Pennsylvanian of Illinois, may well be early ancestors of the frogs.

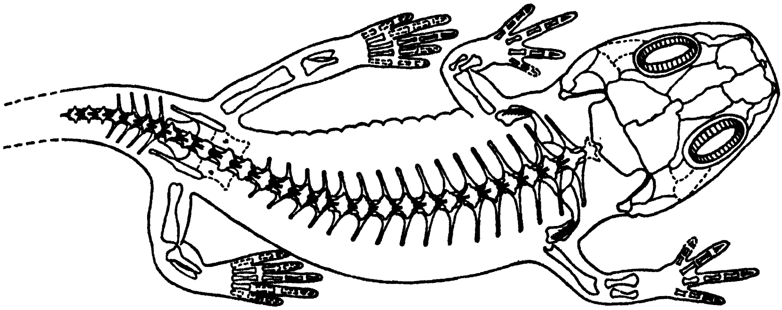


FIG. 119.—*Miobatrachus*, a Pennsylvanian amphibian apparently ancestral to the frogs, about twice natural size. (From Watson.)

The general structure of the body is in most respects similar to that of small labyrinthodonts. The vertebrae are, however, unusual. The neural arches have bases which extend far down over the area in which centra would normally be expected; beneath them are small blocks, apparently representing reduced intercentra and (more doubtfully) pleurocentra. This modification from the labyrinthodont vertebral pattern is exactly that expected in an ancestral frog. Confirmation is given to this suggestion of anuran ancestry in the structure of the skull. It is still adequately roofed, but there have already been lost most of the elements which are missing in modern frogs. The Anura, it would seem, are aberrant descendants of the labyrinthodonts, modestly successful today while their more spectacular relatives have long since become extinct.

Ancient lepospondyls.—We have distinguished from the apsidospondylous type of vertebrae seen in labyrinthodonts and (in modified form) in anurans, a lepospondylous type, in which arch-centra preformed in cartilage do not occur; instead, the centrum forms directly as a bony cylinder around the notochord. Such vertebrae are found today in the salamanders and Apoda; in the late Paleozoic, lepospondyls were numerous and appear to belong to three ordinal types—Aistopoda, Nectridia, and Microsauria. The lepospondyls are known from rocks of early Mississippian age; all three orders flourished greatly in the coal swamps of the Pennsylvanian; a few forms only remained in the Lower Permian; and none of the ancient groups has been found in later periods. These lepospondyls were animals of modest size. Most were but a few inches long; the largest, a foot or two, at the most.

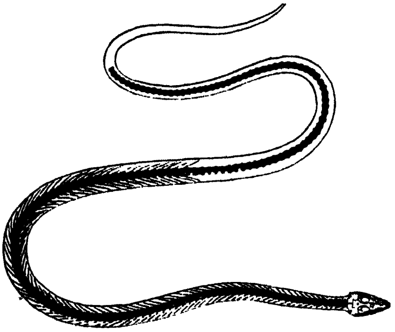


Fig. 120.—*Ophiderpeton*, a snakelike Pennsylvanian lepospondyl, estimated length about 2½ feet. (After Fritsch.)

The order Aistopoda includes but a small number of Carboniferous genera, such as *Ophiderpeton* (Fig. 120) and *Dolichosoma*, in which the limbs had been lost and an elongate snakelike body developed, sometimes with over one hundred vertebrae; there may be short forked ribs of unusual structure. The skull construction is imperfectly known, but the pattern certainly differed considerably from that of more normal groups.

A more varied series of amphibians is that included in the Nectridia. Its members are characterized by the fact that the caudal vertebrae (Fig. 95, *D*) had expanded, fan-shaped neural and haemal spines which opposed one another symmetrically, so that it is often difficult at first glance to tell which is the top and which the bottom of the body. The nectridians diverged into two very distinct types in the Pennsylvanian. In such forms as little *Sauropleura* (Fig. 121) the body was very long, and, as in the aistopods, the limbs had been almost or entirely lost, while the skull was long and pointed. These eel-like types were locally very abundant in the Coal Measures swamps.

A second group of nectridians were forms with small limbs and with grotesque "horned" skulls. *Diplocaulus* (Fig. 122) of the Lower Permian was the last and most highly specialized. The body in some cases was 2 feet or so in length. This late lepospondyl exhibits a series of degenerative changes paralleling those seen in the later labyrinthodonts. As in stereospondyls, there were a large parasphenoid and huge interpterygoid vacuities; two very distinct condyles were developed; the braincase was almost unossified; and the skull as a whole was very much flattened. The greatest specialization lay in the fact that the tabulars were, so to speak, pulled out backward and laterally to form the major part of huge hornlike extensions of the skull roof. The jaws, however, had not elongated and lay far forward on the under side of the skull; while the eyes also had retained their anterior position but looked directly up out of the flat skull roof. The limbs were quite small, and the clavicles and interclavicle expanded into huge flat plates. Obviously, this grotesque creature was a bottom dweller; the whole body may have been so broad and flat that a skatelike up-and-down undulation of the body was possible.

Several related forms, morphologically ancestral to *Diplocaulus*, are found in the Pennsylvanian. In these the "horns" were not so long, the skull a bit higher, the interpterygoid vacuities not so large, the limbs not so disproportionately small, and the body less flattened. In every way they suggest that here, as in other groups, descent can be traced back to a form with a structure comparable (except in the vertebrae) with that found in early labyrinthodonts.

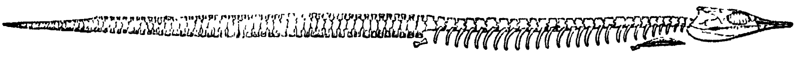


FIG. 121.—*Sauropleura*, a snakelike Carboniferous nectridian. About 7½ inches long. (After Steen.)

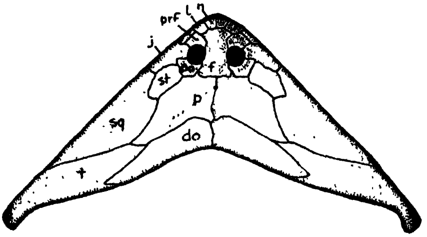


FIG. 122

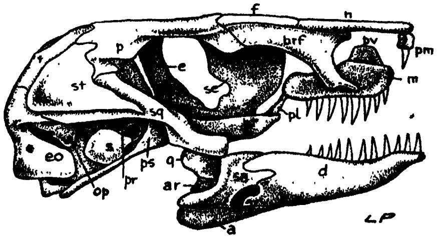


FIG. 123

FIG. 122.—*Left*, dorsal view of the skull of *Diplocaulus*, a "horned" Permian lepospondyl. About ⅛ natural size. (After Williston.)

FIG. 123.—*Right*, *Lysorophus*, a Permian microsaur, possibly ancestral to the Apoda; about three times natural size. For abbreviations see Figure 96. (After Sollas.)

A final group of ancient lepospondyls is that of the Microsauria. This term, "little reptiles," is hardly appropriate; for, although some earlier writers considered them as reptile relatives, their affinities lie rather with the modern salamanders and Apoda. As with the other lepospondyls, the peak of development of microsaurs lay in the Pennsylvanian, and there were but a few early Permian survivors. Microsaurs generally retained a rather normal type of body build, as seen in *Microbrachis* (Fig. 124). There are variations in skull structure, but a basic type appears to be shown in such forms as *Euryodus* (Fig. 125) and *Gymnarthrus*. As may be observed, the elements present are for the most part comparable with those of labyrinthodonts. The temporal region at the side of the skull table appears to offer diagnostic features. This area in labyrinthodonts we have seen to be occupied by a row of two or even three bones—intertemporal, supratemporal, and tabular (cf. Fig. 96); in microsaurs, in the same area, we find only a single large element, provisionally identified with the supratemporal.

Microsaurs varied considerably in structure; one of those most widely divergent from the primitive pattern was *Lysorophus* (Figs. 95, 123) of the Lower Permian, which appears to have dwelt in or about pools of water. This genus had paralleled aistopods and some nectridians in limb reduction; the size and proportions are much like those of a large angleworm. The skull is much modified. In contrast to almost all other Paleozoic amphibians, there was no pineal opening; and the skull was no longer completely roofed, for most of the circumorbital bones were gone and the orbit was open below. The parasphenoid was large, as in most degenerate amphibian types, but the occipital condyle had remained single. In the throat the branchial arches were large and ossified, suggesting that this form retained gill breathing throughout life—a feature probably true of many other lepospondyls. Forms apparently related to *Lysorophus* were already present in the Mississippian; these genera, however, still had a completely roofed skull comparable to that of other microsaurs.

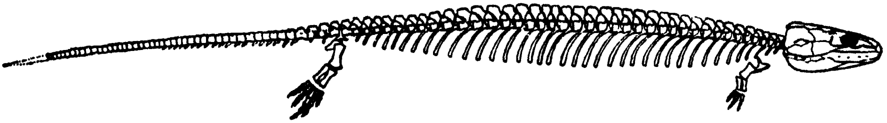


FIG. 124.—*Microbrachis*, a late Pennsylvanian microsaur, about natural size. (From Steen.)

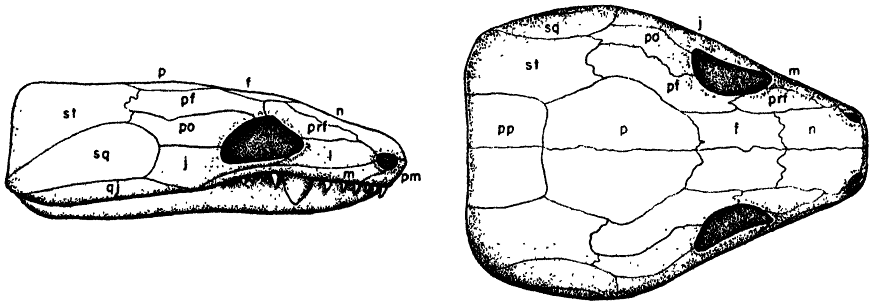


FIG. 125.—The skull of *Euryodus*, an early Permian microsaur, in dorsal and lateral views, about twice natural size. For abbreviations see Figure 96. (After Olson.)

These varied lepospondyls were an important factor in the life of the Carboniferous. The labyrinthodonts supplied the larger and more spectacular members of the amphibian fauna; the little lepospondyls, however, appear to have been much more abundant in the coal-swamp pools. They are obviously a very ancient group, as suggested by the fact that there were already widely divergent types among them when they first appeared in the Mississippian. The very different vertebral structure indicates that they cannot have been derived from true labyrinthodonts and that the two groups must have become distinct at an early Devonian stage of amphibian evolution. It is not impossible that the ichthyostegids were close to the point of departure of the lepospondyls from the early labyrinthodonts.

The Salamanders and Apoda.—The newts and salamanders included in the order Urodela possess, in common with the frogs, a long series of characters, listed in an earlier section, which are indicative of a "phyletic drift" toward skeletal degeneracy. They differ markedly, however, from the anurans in many respects. The vertebrae are built essentially on the pattern seen in Paleozoic lepospondyls and contrast with those of anurans. In most salamanders, limbs of normal build are present, although they are usually rather small. Externally the salamanders, with a long body and well-developed tail, resemble primitive amphibian types. Internally, however, the skeleton shows many modifications and regressions. The limb girdles are largely cartilaginous (there is only one ossification in the shoulder), and the dermal shoulder girdle has disappeared completely. There is usually a well-developed branchial arch skeleton, for there is a general tendency in the group to persist in a water-living mode of life; and a number of types never leave the water, continuing to breathe with gills throughout life.

There are a number of salamanders known from the Tertiary; it is of interest that one large Miocene form (*Andrias*) was, some hundreds of years ago, regarded as the skeleton of a poor human sinner drowned in the flood, "Homo diluvii testis." The oldest-known salamander is a Lower Cretaceous genus; there is no record at all of urodeles or possible ancestors in the Jurassic or Triassic. Their origin is thus not positively known. It seems certain, however, that they are derived from some group of lepospondyls. The aistopods and nectridians are apparently ruled out by too great specialization, but some of the more generalized microsaurs show a skull pattern from which that of urodeles may have been derived.

The Apoda (or Gymnophiona) include a few genera of small, tropical, burrowing forms of very peculiar build. There are no limbs, and the general appearance is that of a large earthworm. Alone among living forms the Apoda have retained scales, although these are small and buried in folds of skin. The skull is technically roofed, for there is a complete covering to the top and sides. But there has been a considerable loss of elements and much change in the shape and position of those remaining. The orbits are very small, for these forms are practically blind; and there are, instead, pits lodging tentacles which functionally take their place. This solidly built little head is quite possibly derived from one in which much of the dermal covering had been lost; it seems likely that there has been a secondary fusion of the remaining elements, resulting in the formation of a more effective burrowing organ.

There are no known fossil representatives of the group to help bridge the long time interval back to the Permian, when there existed lepospondyls from which (as indicated by vertebral structure) the Apoda might have arisen. Despite this, one may believe with fair confidence that the microsaur *Lysorophus* may represent the ancestors of the Apoda. *Lysorophus* was, like the modern forms, small and wormlike and, as we have seen, had a peculiarly modified skull which appears to agree in many characters with that of the Apoda. *Lysorophus* we believe to have been a water dweller; transitional habits are seen in one apodan genus which inhabits water-filled burrows along pond margins.

CHAPTER 7

PRIMITIVE REPTILES

THERE is no more interesting story in the fossil record than that of the rise and fall of the reptiles. Springing from the primitive amphibians during the Carboniferous, they became the dominating group of vertebrates during the whole of the Mesozoic and gave rise to many curious and spectacular types. Now they are in decay; but it must not be forgotten that the birds and mammals which have triumphed over them are their descendants.

Class characteristics.—Reptiles have numerous features which serve to distinguish them from other tetrapods. Like the amphibians, but unlike the birds and mammals, they are cold-blooded, that is, there is no effective mechanism for the regulation of body heat and, in consequence, the activity of the animal varies with the temperature. Because of this, reptiles are characteristically tropical forms and become increasingly rare as we proceed toward the polar regions.

The most distinctive feature of the reptiles, as contrasted with amphibians, is the type of developmental history, for the egg can be laid on land. It is protected against drying and against mechanical injury by a series of membranes and fluids surrounding the developing embryo. Further protection is afforded by a firm shell. This shell, however, is porous; and one of the membranes within acts as an embryonic lung, extracting oxygen from the air. Since the young reptiles must emerge fully equipped for life on land, considerable growth is necessary; this is rendered possible because the egg is large and contains a good supply of nourishing yolk and albumen.

The initiation of this new mode of development was an epochal event in vertebrate history. Only with the appearance of the amniote egg did a truly terrestrial existence become possible. The amphibian is, from one point of view, nothing but a rather aberrant fish type. It may exist for a time on land, but it is chained to the water; it cannot stray far from that element and must pass its early life as an aquatic form. The reptile, however, can develop directly into a terrestrial animal, and a much better opportunity is given for the perfection of a higher type of organization. This organization is apparent in every part of the body—in skeleton, in muscle, in the circulatory system. Even in the brain the reptile is on a higher plane; for, while this structure is still small compared with that of birds or mammals, it is, nevertheless, a much better organ than the amphibian brain; in its small cerebral hemispheres appear for the first time the rudiments of the higher mental centers which have become predominant in the brains of mammals.

Reptiles living today can easily be distinguished from amphibians by means of soft parts; and among living types it is also feasible to distinguish between these classes by means of skeletal features. Reptiles, for example, have but one condyle on the skull, modern amphibians two; reptiles typically have five toes in the manus, living amphibians four or less. The sacrum in reptiles includes at least two vertebrae, whereas there is but one in amphibians.

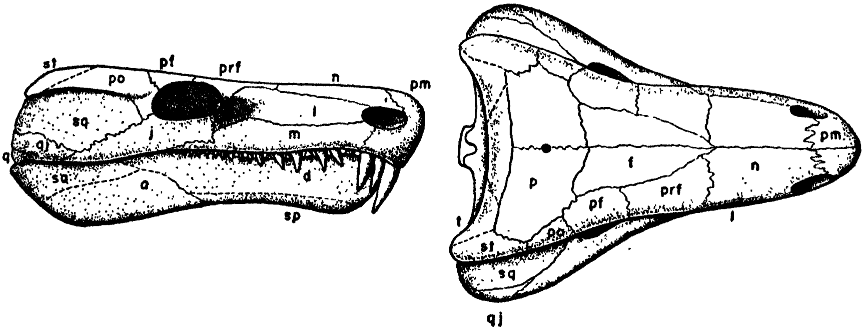


FIG. 126 FIG. 127

FIGS. 126, 127.—*Limnoscelis*, a primitive reptile; skull in dorsal and lateral views; length about 10½ inches. For abbreviations see Figure 96. (After Williston.)

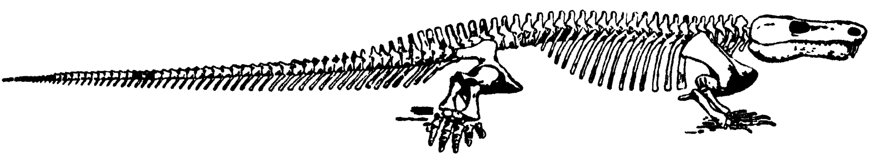


FIG. 128.—The skeleton of *Limnoscelis*; length about 5 feet. (From Williston.)

But the fossil evidence obliterates these and other supposed differences. Primitive Paleozoic reptiles and some of the earliest amphibians were so similar in their skeletons that (as was seen in the case of *Seymouria*) it is almost impossible to tell when we have crossed the boundary between the two classes.

Structure of primitive reptiles.—As an introduction to the study of the reptiles we may first consider the structure of such primitive types as *Limnoscelis* (Figs. 126, 127, 128), *Captorhinus* (Fig. 129), and *Labidosaurus* (Fig. 130) and then discuss briefly some of the many variations to be found in the reptilian orders.

These genera are from the Lower Permian of the American Southwest and are thus among the oldest reptiles of which we have any detailed knowledge. They are members of the order Cotylosauria. *Limnoscelis* was about 5 feet in length (including a long tail) and rather clumsy in build; the other genera were smaller and with less massive limbs. *Limnoscelis* appears to have been a carnivore of some sort; the others, in addition to exceptionally large teeth in the premaxilla, have an unusual condition in the presence of several rows of cheek teeth, which indicate some peculiarity in their diet (hard-shelled invertebrates?). *Limnoscelis* appears to be a very primitive reptile, but the skull structure is incompletely known; *Captorhinus* and *Labidosaurus* are somewhat more advanced.

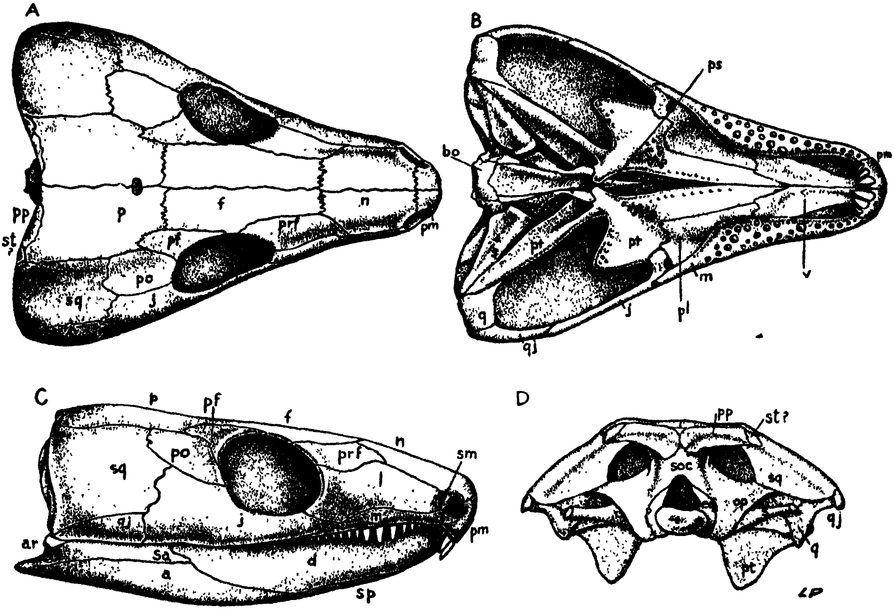


FIG. 129.—*Captorhinus*, a cotylosaur. *A*, Dorsal; *B*, ventral; *C*, lateral; *D*, occipital views of skull. Length of original about 2¾ inches. For abbreviations see Figure 96. (Data from Price.)

The skull in these reptiles, as in this class in general, has remained rather high and narrow, in contrast to the flattening prevalent among almost all amphibians. Much of the skull pattern seen in primitive amphibians is repeated in primitive reptiles, but there are noteworthy differences and evolutionary advances. One prominent change is the elimination of the characteristic otic notch of amphibians. In most reptiles the eardrum has moved backward and downward to a position on the side of the head above the jaw articulation. In many groups, including some cotylosaurs (cf. Fig. 134) this position is marked by a new type of otic notch—a concavity in the posterior margin of the bones covering the cheek; in the forms here discussed this is not developed. In *Limnoscelis* an anteroposterior ridge is found at the edge of the skull table, marking the place where the edges of the former notch have joined; in *Captorhinus* this has been obliterated. The elimination of the otic notch is mechanically advantageous, giving to the region of the jaw articulation vertical support and suspension from the skull-roof and braincase region.

The bony pattern of the skull table has somewhat altered in primitive reptiles. We have noted previously the gradual reduction of the postparietals from the crossopterygian condition in which they extend perhaps a third the length of the skull (Fig. 62) to their relatively modest size in most labyrinthodonts. In early reptiles they are still further limited in extent, and in later types they will be seen to disappear completely or to abandon the roof for a position on the occipital surface. The tabulars have undergone a similar reduction. In amphibians the skull table was bordered laterally by a supratemporal and frequently an intertemporal as well. The latter has never been observed in reptiles; the former is present as a small structure in a number of reptiles (Figs. 127, 134, 148, 220) but has generally disappeared.

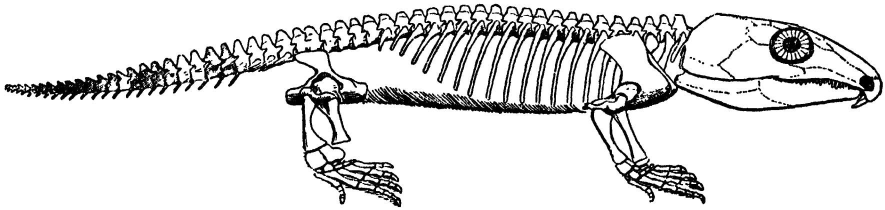


FIG. 130.—*Labidosaurus*, a Lower Permian cotylosaur; original about 26 inches long. (From Williston.)

Apart from the skull-table and otic-notch regions, the roofing bones of early reptiles are very similar to those of the more generalized labyrinthodonts. The pineal opening is generally present, and the lacrimal bone extends the full distance from orbit to naris.

The palate is readily comparable with that of labyrinthodonts. *Captorhinus* is specialized in its maxillary dentition, but normally there is a single row of marginal teeth. There are slender vomers separating the choanae, palatines, and small ectopterygoids. The prominent pterygoid (above which lies a rodlike epipterygoid) articulates movably with a basal process of the braincase. Narrow interpterygoid vacuities separate the pterygoids from one another and from a slender parasphenoid lying beneath the front end of the braincase. There is a large vertically placed quadrate. Two features, however, differ from those of amphibians. The old system of palatal fangs with accompanying pits is not repeated here, although the palatal bones are frequently tooth-bearing; and the pterygoid bears a prominent transverse flange, often tipped by a row of teeth. This type of palate is present today relatively unchanged in *Sphenodon* (Fig. 166) and many lizards.

The braincase is relatively high and narrow, in contrast with the flat condition developed in most amphibians. It is well ossified, containing the same elements found in primitive amphibians. Posteriorly, a series of occipital and otic bones form well-developed walls for the brain cavity, and anteriorly there is a sphenethmoid element. Midway of the length of the braincase, above the region of the palatal articulation, there is, however, a large unossified gap in the lateral walls. There is here, as in all typical reptiles, a single occipital condyle. With the closure of the otic notch, stout "paroccipital" processes of the opisthotic bones run laterally to brace the region of the jaw joint. The large openings left above these processes may remain open (as in *Captorhinus*) or may be covered by flanges descending from the skull roof. There is typically a large stapes running laterally from the ear capsule to the region behind the quadrate, where the eardrum was situated.

The lower jaw is generally comparable to that of amphibians, but the number of elements is reduced. There is but a single splenial and one coronoid (rarely two).

√The vertebrae of cotylosaurs are almost identical in structure with those of the *Seymouria* group (Fig. 94), strongly suggesting their relationship. The centrum, a stout cylindrical structure pierced for the notochord, is the element frequently termed pleurocentrum in amphibians; the intercentrum is present as a crescent of modest size. A diagnostic feature of cotylosaurs (but one found in a few other early reptiles and in *Seymouria* as well) is the fact that the zygapophyses are placed far apart laterally and the supporting neural arches have a pronounced swollen appearance, with a convex outline when seen in end-view. There is still little regional differentiation, for ribs may be present throughout the trunk and the base of the tail. The anterior ribs are double-headed, the capitulum attaching to the intercentrum, the tubercle to the transverse process; more posteriorly the two heads tend to fuse, the capitular attachment transferring upward onto the centrum near the base of the neural arch.

The limbs are of the short, stubby type found in many primitive amphibians, with the proximal elements projecting at right angles to the body. The massive shoulder girdle is close behind the head, there being almost no neck. It is very similar in many respects to that of such an amphibian as *Eryops*. However, in reptiles the ventral part of the primary girdle (Fig. 131, *A*) is (in contrast with almost every amphibian group) a separate coracoid element, and the interclavicle has a long posterior stem for the attachment of powerful breast muscles; such a stem was present in seymouriamorphs but not in other amphibians. In most primitive reptiles the cleithrum is present, although reduced. The pelvic girdle in primitive reptiles (Fig. 131, *C*) consists of the usual three elements; but the ilium is larger and more expanded than in amphibians, a feature presumably related to greater walking powers and increased musculature.

The limb bones are in many respects similar to those of a well-developed ancient amphibian such as *Eryops*. Most early reptiles possess an entepicondylar foramen, an opening for nerve and blood vessels on the back (or inner) side of the humerus near the distal end. Such a structure is found in a few primitive or reptile-like amphibians but is generally absent in that class. In primitive reptiles the carpals (Fig. 226) are, for the most part, comparable to those of early amphibians; however, there are never more than two central elements of the original four. In the tarsals (Fig. 227) the centralia are similarly reduced. Here, however, another and more important change in foot structure has occurred. The inner proximal element—the tibiale—has been eliminated, and the tibia now articulates with the inner margin of the intermedium (the mammalian astragalus). This permits the foot to swing more readily into a forward position and gives a very free movement between shank and foot. There are primitively five toes in both front and hind feet and a phalangeal formula of 2–3–4–5–3(4). Only in seymouriamorphs have we seen among amphibians a five-toed manus or as high a phalangeal formula.

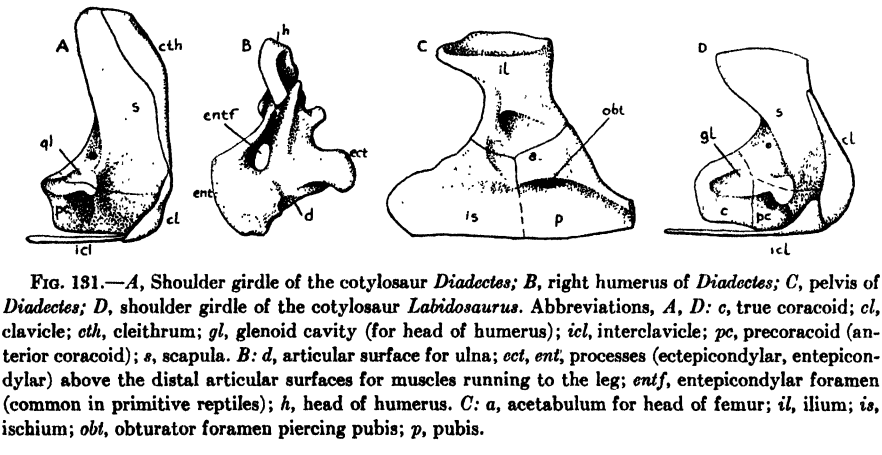


FIG. 131.—*A*, Shoulder girdle of the cotylosaur *Diadectes; B*, right humerus of *Diadectes; C*, pelvis of *Diadectes; D*, shoulder girdle of the cotylosaur *Labidosaurus*. Abbreviations, *A, D: c*, true coracoid; *cl*, clavicle; *cth*, cleithrum; *gl*, glenoid cavity (for head of humerus); *icl*, interclavicle; *pc*, precoracoid (anterior coracoid); *s*, scapula. *B: d*, articular surface for ulna; *ect, ent*, processes (ectepicondylar, entepicondylar) above the distal articular surfaces for muscles running to the leg; *entf*, entepicondylar foramen (common in primitive reptiles); *h*, head of humerus. *C: a*, acetabulum for head of femur; *il*, ilium; *is*, ischium; *obt*, obturator foramen piercing pubis; *p*, pubis.

From such primitive structural types as these early cotylosaurs there have been enormous variations among later orders of reptiles. The development of bipeds from quadrupeds and the evolution of flying forms and of many marine types have caused many startling changes in the general body organization. We shall here outline some of the main trends.

The reptile skull.—The skull in reptiles has tended in general to become progressively higher and narrower in shape, in contrast with the flattening found among amphibians. Many of the dermal roofing elements may disappear. The supratemporal and, later, the tabulars and postparietals tend to become reduced and lost. The pineal may be absent, and there may be considerable variation in the bones about the orbits.

Especially to be noted is an interesting series of variations in the cheek region of the skull. The temporal muscles closing the jaws have their attachment under the bones covering this region. It appears that when a muscle arises from a broad plate of bone, its action is facilitated if an opening (fenestra) develops through which the muscle may bulge when contracted. In correlation with this we find that in most later reptiles the cheek is fenestrated, that is, openings appear between various bones. These fenestrae vary considerably, apparently being related to different developments of the temporal muscles (Fig. 132). Frequently there is but one opening. In some cases this is high up on the skull and bounded below by the squamosal and postorbital; in others (mammal-like forms) it is low on the side, and these two bones are in contact above it. These two types of opening are termed the upper (superior) and lateral temporal vacuities. In a large number of types (the crocodiles and dinosaurs, for example) both openings may be present, with the postorbital and squamosal meeting between the two.

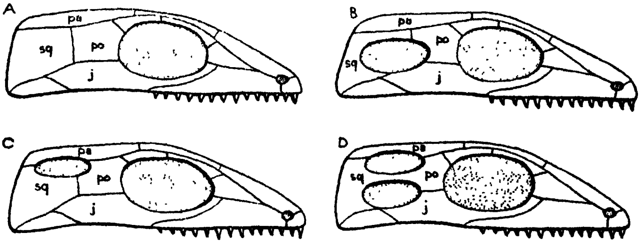


Fig. 132.—Diagrammatic side views of reptilian skulls to show various types of temporal opening. *A*, No opening—"anapsid" condition; *B*, a lower opening with postorbital and squamosal meeting above—"synapsid" condition; *C*, an upper opening with postorbital and squamosal meeting below—"parapsid" condition; *D*, both openings present—"diapsid" condition. Abbreviations: *j*, Jugal; *pa*, parietal; *po*, postorbital; *sq*, squamosal.

There are many variations in the palate. In some types the palatal bones may fuse into a nearly solid plate. In several groups the internal nostrils may be shifted back from their original anterior position by the construction of a shelf—a secondary palate—in the roof of the mouth.

Axial skeleton.—In the backbone there is a universal tendency for the reduction of the intercentra. Even in most Permian forms they are merely small ventral crescents, and they usually disappear completely in Mesozoic types. The true centra tend to lengthen. They are primitively hollow at both ends (amphicoelous), but the opening for the notochord usually disappears; the ends may be flush across (platycoelous), while in many cases articulations are developed between successive centra, one end being hollowed, the other swelling out to fit into this socket. Various terms have been devised to describe this and other conditions. If, for example, a vertebra is concave in front and convex behind, it may be termed procoelous; the opposite condition is opisthocoelous.

The ribs vary greatly in structure (cf. Figs. 146, 175, 215). The attachments of the two heads may shift, or a single-headed condition, with attachment either to centrum or to neural arch, may result. With the development of a true neck in most reptiles, the ribs in this region may shorten or even disappear, and a well-marked cervical region be formed. The number of sacral ribs tends to increase in large forms and particularly in bipedal types.

In addition to the ventral continuation of the ordinary ribs, reptiles often have independent structures called "abdominal ribs"—dermal, bony, splint-like elements, ranged along the belly in V-shaped rows. These structures are seemingly the last remnants of the old fish scales which were developed in amphibians in a similar position on the under side of the body. While reptiles are scaled (in contrast with living amphibians), the scales are really horny scutes (although plates of bone often develop beneath them) and are not homologous with fish scales.

Limbs.—There is, of course, much variation in the limb structure. In the shoulder girdle the cleithrum tends to disappear very early in reptile history (it is found in but a few Triassic forms and in none today), and the other dermal elements may be lost as well. In most reptiles a scapula and a single coracoid constitute the elements of the primary girdle; but in one major group (mammal-like reptiles) a second, posterior, coracoid element is added (Fig. 222). The peculiar screw-shaped glenoid of primitive types disappears by the close of Permian times. There is never any change in the number of pelvic bones, but in many cases a fenestration of the ventral plate occurs in relation to the origin of a large limb muscle, a development comparable to the fenestration seen in the skull (cf. Figs. 138, *C;* 158, 223, *B, C*).

The limb bones in general tend to become much slimmer than in primitive forms, and many variations in structure occur in relation to varied locomotor needs. In the humerus the entepicondylar foramen characteristic of primitive reptiles usually disappears, but there often develops an ectepicondylar foramen on the outer side of the distal end of the bone (Fig. 224, *B, C*). Reduction takes place in carpus and tarsus (cf. Figs. 226, *A;* 227, *A;* etc.). There is usually but a single centrale, and the outer distal element usually disappears in both carpus and tarsus. The number of joints in the toes is, in general, remarkably uniform. The outer toe, especially in the hind foot, tends to be set off at an angle and may disappear. In bipeds among the dinosaurs there are strong tendencies for reduction in number of toes, and the limbs may, of course, be strongly modified to form fins or paddles.

Reptile radiation (Fig. 133).—The earliest remains of reptiles are found in the Pennsylvanian. Known specimens from that period are few; but, since practically all our knowledge of Carboniferous fossils is gained from coal-swamp deposits, we know nothing of the life of higher and dryer regions where reptiles might well have already been numerous. Dating from the end of the Pennsylvanian and the beginning of Permian times are deposits (red beds) of a more terrestrial type in which are found abundant reptiles, including not only primitive cotylosaurs but also more advanced types. Amphibians were still numerous at that time; but long before the close of the Permian they had been pushed into the background, and the radiation of the reptiles was under way. Almost every known reptilian group made its appearance before the end of the Triassic. In the Jurassic and Cretaceous these groups increased in size, in abundance, and in diversity. Toward the close of the Cretaceous, however, the great reptilian orders waned; and the beginning of the Cenozoic is marked by the end of the reptilian dynasties and the radiation of the mammals. Only a few reptilian groups have survived—the lizards and snakes, the turtles, the crocodiles, and the rhynchocephalian *Sphenodon*.

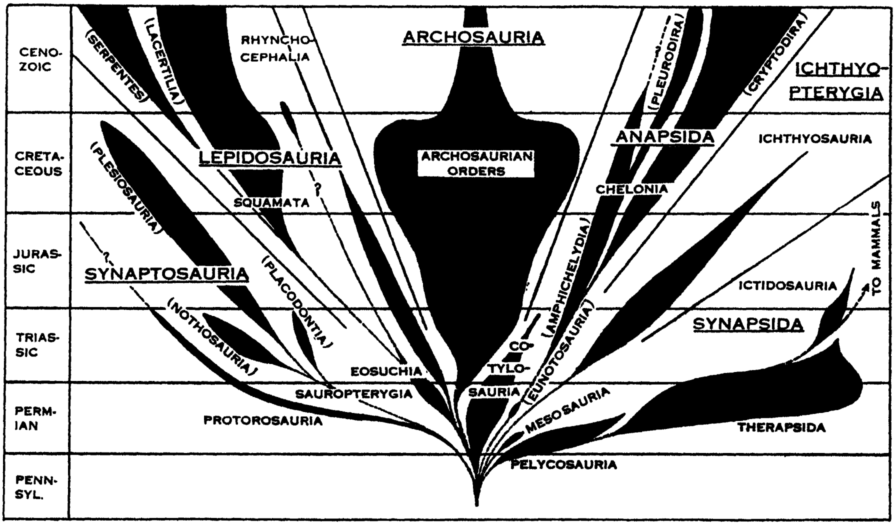


FIG. 133.—The phylogeny of reptiles. (The archosaurs are shown separately in Fig. 178.)

These varied reptilian types have been arranged in from fifteen to twenty or more orders by different authors. It is probable that they did not all spring directly and independently from the base of the reptile stem, and various workers have attempted to assemble larger groups of presumably common parentage as subclasses or superorders. It is difficult to select a proper basis for such classification; the most obvious differences between groups lie in the varied construction of the limbs and other superficial features which are closely related to environmental adaptations and are hence untrustworthy (seagoing reptiles, for example, are all likely to develop paddle-like legs, but this means merely convergent adaptation and not real relationship). It was early suggested that the nature of the temporal openings was a better criterion, and attempts to work out reptilian phylogenies have been based mainly on this feature. It was once thought that all reptiles originally had two temporal openings, and hence forms with two openings (or two bars across the temple, which amounts to the same thing) were termed "diapsid" (two-arched); and forms with one opening (in which it was presumed that the two openings had fused into one), "synapsid" (fused-arched) reptiles. But it soon became obvious that this division was inadequate. Truly primitive forms must have possessed a completely roofed skull like that of their amphibian ancestors, and for this condition the term "anapsid" was coined. Further, the single opening found in a number of groups is obviously not homologous throughout, being sometimes a superior, sometimes a lateral, one; and temporal fenestrae may shift in position or become secondarily closed. These structures may be used for purposes of classification—but must be used, like any other single character, with caution.

Cotylosaurs.—The primitive reptiles described above belong to the order Cotylosauria, the basal stock from which it is believed the other reptilian orders have arisen—a group appropriately termed the "stem reptiles." Certain incomplete reptilian remains from the typical Pennsylvanian presumably pertain to cotylosaurs. At the very end of that period and the lower part of the Permian they had become common and diversified. But other reptilian groups had already evolved from them, and, from that time on, the cotylosaurs began steadily to lose in importance. Comparatively few were left in the later Permian, and in the late Triassic the group became entirely extinct.

As is the case with primitive ancestors of any group, a "stem reptile" is difficult to define; cotylosaurs are distinguishable mainly by the presence of primitive and comparatively unspecialized features—the lack of the peculiarities found in derived groups. The one certain criterion is the fact that the roof of the skull is not pierced by fenestrae in the temporal region. This is the anapsid condition, and the stem reptiles may be placed in a subclass Anapsida, in which the turtles are perhaps to be included as well.

The cotylosaur limbs are usually short and stubby, the feet generally little modified. The dermal shoulder girdle is complete, and the cleithrum often of considerable size. There are usually two sacral ribs. Previously noted were the swollen neural arches which aid in distinguishing cotylosaurs from nearly all other reptile types.

The *Seymouria* group, here considered as reptile-like amphibians rather than as true reptiles, are often included in the cotylosaurs. Apart from these forms, the known cotylosaurs can be conveniently grouped into two suborders—Captorhinomorpha and Diadectomorpha.

Captorhinomorphs.—The cotylosaurs so far mentioned are all members of the captorhinomorph group; *Captorhinus* (Fig. 129) and *Labidosaurus* (Fig. 130) are the best-known members, but they are rather advanced in structure and with a specialized dentition; *Limnoscelis* (Figs. 126, 128) is much more primitive in general organization. These genera are of early Permian age and are too late in time to be truly ancestral reptiles, for members of other reptile orders were already in existence. It appears likely, however, that the history of captorhinomorphs extends well back into the Carboniferous. *Solenodonsaurus*, an incompletely known reptile from the Upper Pennsylvanian of Europe, is probably an early captorhinomorph, and there are other fragmentary specimens of this age. This subordinal group may lie close to the stem of the reptiles, if, indeed, the stem reptile itself was not a member of it. But captorhinomorphs themselves were destined to early extinction, for none is present beyond the Lower (or possibly Middle) Permian.

Diadectomorphs.—We have noted that with the disappearance of the amphibian type of otic notch, the eardrum has generally shifted to a position above the jaw articulation. Here it lies just behind the posterior edge of the cheek region of the skull. In some cases (as in captorhinomorphs) this position of the drum has no influence on skull contours; in others we find its position marked by a curved excavation—a new type of otic notch—in the posterior margin of the cheek region. This condition is, among cotylosaurus, diagnostic of the Diadectomorpha.

Diadectes (Fig. 134) is the type of the diadectomorphs; this genus and its close relatives were common animals in the latest Pennsylvanian and early Permian of North America and Europe. The diadectids were, in general, large animals for their day, with a length of 5 feet or more. The postcranial skeleton was heavily built and rather similar to that of *Limnoscelis* or even *Seymouria*. The skull appears to have been highly modified, although showing a number of primitive features. It is short and massive with little elongation of the face. Tabulars and postparietals appear to have been, for a reptile, rather well developed, and there appears to be a prominent supratemporal. The teeth, confined to the jaw margins, are peculiarly modified. The front teeth are chisel-like cropping structures, the cheek teeth a battery of transversely widened grinders with several cusps. Posteriorly the cheek is deeply excavated for the eardrum; the powerful quadrate, binding jaw to braincase, is exposed in the borders of this notch.

A more advanced type, which appears to be closely related to the diadectids, although not directly descended from them, is that of the pareiasaurs of the Middle and Upper Permian of Europe and Africa (Fig. 136). These were the largest of cotylosaurs, ranging up to 10 feet or so in length. With increase in size, the problem of weight support becomes a serious one. It would have been physically impossible for such a large animal to have walked with its limbs spread out at the sides, and in this connection we find that in pareiasaurs the limbs had rotated in toward the body and bore the weight more vertically. This change in pose was accompanied by changes in the limb bones similar to those which we shall see in the reptilian ancestors of mammals. While the feet of most cotylosaurs were of a very primitive character, those of the pareiasaurs tended to be considerably modified; the fifth toe, for example, tended to be reduced or lost in many cases.

The skull was very large and grotesque, often with warty or hornlike protuberances. The teeth along the margins of the mouth were serrated and leaf-shaped, and there were rows of small teeth on the palate. No excavation for the eardrum comparable to that of *Diadectes* appears to be present. In reality, however, it is well developed but covered superficially by a great expansion of the cheek plate, so that this notch faced backward rather than laterally. These forms were obviously noncarnivorous, slow, and harmless reptiles, and for defense there were usually plates of bone studded along the back.

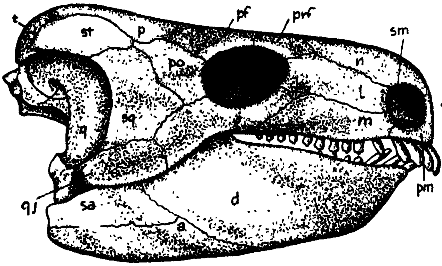


FIG. 134

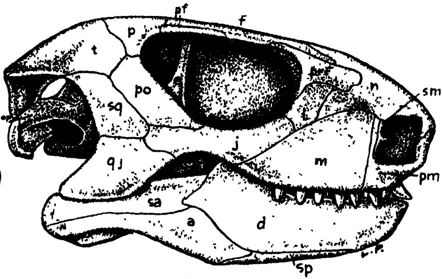


FIG. 135

FIG. 134.—*Diadectes*, an early Permian cotylosaur, skull length about 8 inches. (After Williston.)

FIG. 135.—*Procolophon* of the Lower Triassic of South Africa, skull length about 2 inches. For abbreviations see Figure 96 (After Watson.)

Numerous remains of pareiasaurs, such as *Bradysaurus*, have been found in the Middle Permian beds of South Africa, the skeletons often complete and right side up in the position in which they presumably became mired in their native swamps. In later Permian times they became rarer in South Africa but had spread to Europe, where skulls and skeletons have been found in Russia and Scotland.

A final group of diadectomorphs, and the last survivors of all the cotylosaurs, was that including *Procolophon* (Fig. 135) and its allies of the Triassic. These were small reptiles, usually a foot or two in length, rather slim-limbed and (much as in *Diadectes*) with transversely expanded cheek teeth. The otic notch was exceedingly well developed. Smaller and swifter than the pareiasaurs, they lacked armor for protection against carnivores. In some early Triassic strata they are comparatively abundant, but by the close of the period these last stragglers of the cotylosaurs had vanished.

The feeding habits of the diadectomorphs have been a matter of discussion. Obviously they were not carnivores. A mollusk diet has been suggested in the case of *Diadectes,* but the teeth show a type of wear suggesting chewing rather than shell-crushing functions, and the relatively feeble teeth of the other members of the group are not adapted to this type of food material. Herbivorous habits appear much more likely. There is no reason to believe that any of the early amphibians were plant feeders—apart from larvae and possibly some of the smaller lepospondyls—and the diadectomorphs may have been the first to appear of many successive groups of herbivores developed among land vertebrates.

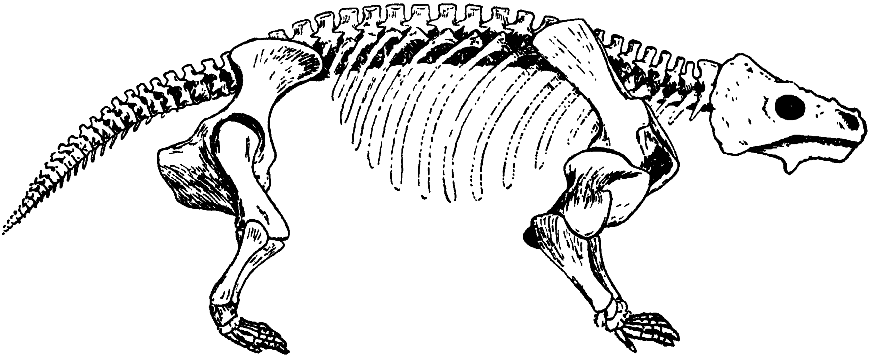


FIG. 136.—The skeleton of the Middle Permian pareiasaur *Bradysaurus;* length about 8 feet. (After Broom.)

It is possible that the diadectomorphs are close to the ancestry of some of the later orders—particularly those groups in which this new type of notch for eardrum support was highly developed. Proof, however, is lacking, for all known diadectomorphs are already highly specialized when we first know them.

Most of the varied cotylosaurs discussed above did not lead to later reptilian types. They appear to represent merely part of an archaic radiation of the reptiles into various modes of life at a very early date, soon after they had shaken off the encumbrances of the old amphibian mode of development. They are very important members of the Permian fauna; for, together with mammal-like forms, they constituted an overwhelming majority of Permian reptile types. But their importance waned rapidly, and they soon gave place to members of a second wave of reptilian radiation which included the orders which were to dominate the Mesozoic.

CHAPTER 8

VARIED REPTILIAN TYPES

THE greater proportion of the Mesozoic and Tertiary reptiles belong to large and important orders which can be assembled more or less satisfactorily into major subclasses of advanced reptiles—Synaptosauria, Lepidosauria, Archosauria, and Synapsida. There remain, however, several orders which occupy isolated positions and seem to represent independent stocks rising directly from the ancestral cotylosaurs. Of such a nature are the turtles, mesosaurs, and ichthyosaurs, which are treated in the present chapter.

Chelonians.—The turtles, forming the order Chelonia, may technically be included as members of the Anapsida, since it is probable that the skull roof, although often emarginated and incomplete, has never developed true temporal openings. In almost every other respect, however, the turtles have departed widely from the structural pattern of their cotylosaur ancestors.

The chelonians are the most bizarre, and yet in many respects the most conservative, of reptilian groups. Because they are still living, turtles are commonplace objects to us; were they entirely extinct, their shells—the most remarkable defensive armor ever assumed by a tetrapod—would be a cause for wonder. From the Triassic the turtles have come down to present times practically unchanged; they have survived all the vicissitudes which have swamped most of the reptilian groups and are in as flourishing a condition today as at any time in the past.

The turtle shell (Fig. 137).—The armor plate of the ordinary modern turtle is composed of two materials—horny scutes representing the ordinary reptilian scales on the surface and bony plates underneath. The arrangement of the outlines of scutes and bones does not coincide; in general, there is an alternating arrangement, which gives greater strength to the combined structure. The scutes are not, of course, preserved in fossils, although the outlines are often indicated by grooves in the bones which lay beneath them.

The bony shell is divisible into a dorsal carapace and a ventral plastron, connected by a bridge at the sides. At the center of the carapace is a row of eight bony neural plates fused to the neural arches of the vertebrae beneath. Lateral to them on either side is a row of longer plates, also eight in number; these are fused to the eight underlying ribs and are hence known as costals.

Circling the edge of the carapace is a ring of small elements—the marginals. In addition, there may be in the central row an extra nuchal element in front of the neurals and a few pygals behind them.

A much smaller number of bony elements is present in the ventral shield—the plastron. Near the front is a median plate—the entoplastron. The other elements, which are paired, consist (from front to back) of epiplastra, hyoplastra, in some primitive types one or two pairs of mesoplastra, then hypoplastra and xiphiplastra.

The shell is widely open in front for the withdrawal of the head and front legs; behind, for the hind legs and the stubby tail.

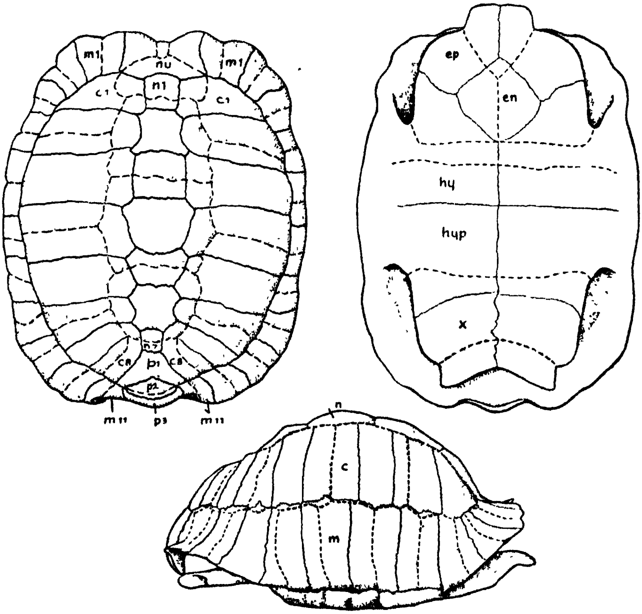


FIG. 137.—*Testudo ammon*, a giant tortoise from the early Tertiary of Egypt. Carapace (*upper left*) plastron (*upper right*), and lateral view, to show shell structure of chelonians. Sutures in solid line; outline of overlying horny scutes in dashed lines. Carapace, bony elements: *c*, costal plates; *m*, marginal plates; *n*, neural plates; *nu*, nuchal; *p*, pygal. Plastron: *en*, entoplastron; *ep*, epiplastra; *hy*, hyoplastra; *hyp*, hypoplastra; *x*, xiphiplastra. Original about 39 inches long. (After Andrews.)

It would seem that the carapace, at least, has arisen through the development of new plates of dermal bone. Such plates are developed in many crocodiles and some lizards, as well as in other groups now extinct. The turtles differ from them in the consolidation of the plates into a complete, compact covering. As regards the plastron, however, it may be that no new elements were needed. The old fish scales had been retained in many primitive reptiles as the so-called "abdominal ribs." It is possible that the turtle plastron for the most part arose by an enlargement and consolidation of these elements. With regard to the front of the plastron, it is interesting to note that the paired epiplastra articulate internally with the scapula, as do the clavicles of ordinary reptiles, while between them the single entoplastron lies in the position of an interclavicle. The anterior elements of the shield thus appear to represent the old dermal shoulder girdle.

Body skeleton.—The backbone is, of course, much modified in connection with the development of the shell. The tail is short and easily tucked away. There are two sacral vertebrae and only ten trunk vertebrae in front of it, all except the first immovably attached to the median plates of the shell. This represents a great shortening of the body from primitive conditions; probably nearly a dozen vertebrae have dropped out. There are eight ribs, fused to the under side of the costal plates; this fusion and that of the neural arches with the median elements effectively brace the shell. There are eight cervicals in the neck; in modern forms, in which the head is withdrawn into the shell, these have very complicated articular arrangements.

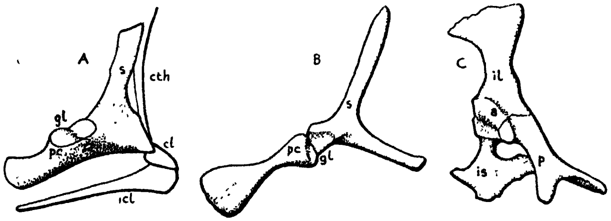


FIG. 138.—Limb girdles in chelonians. *A*, Shoulder girdle of the primitive *Triassochelys*. The girdle is still close to the primitive reptilian type; a cleithrum is present; the dermal elements forming part of the plastron are shown. *B*, Shoulder girdle of *Toxochelys* (Cretaceous). *C*, Pelvic girdle of the Oligocene *Testudo laticunea*. For abbreviations see Figure 131. (*A* after Jaekel; *B*, *C* after Hay.)

Limbs.—The limbs and girdles are of rather peculiar construction, as might be expected from the requirements of a shell-inclosed life. The limbs spread out at the sides, giving a broad trackway and a short stride, much as was the case in the cotylosaurs; and it is not improbable that this old-fashioned method of walking was present in the group when the shell first appeared and has become permanently fixed. In detail, however, the limbs are far from primitive.

In the shoulder girdle the dermal bones have been taken over into the plastron. The primary girdle (Fig. 138, *B*) is a triradiate structure with the glenoid cavity at the union of the branches; the scapula includes a slim ascending blade and a long projection which goes down to touch the clavicles (the epiplastra); while the third prong is a single coracoid. In the pelvic girdle (Fig. 138, *C*) much of the ventral region, instead of being a solid plate of bone, is occupied by a large opening or fenestra which has separated the pubis and ischium almost completely from each other. The feet are quite specialized; notable is a tendency (rather unusual among reptiles) for a general reduction of the number of phalanges in the toes, so that there is never a higher phalangeal formula than 2-3-3-3-3.

Skull (Fig. 139).—The skull is also highly specialized in a number of ways. Modern turtles entirely lack teeth, their function being taken over by a horny beak which sheaths the edges of the jaws. The palatal bones have fused and united so as to give a solid structure quite different from that of primitive reptiles. At the side, the proötic and opisthotic bones of the ear capsule have fused broadly with the quadrate and squamosal, so that the region of the jaw articulation is solidly bound into the braincase. The pineal eye no longer pierces the roof of the skull, and the two external nostrils have a common bony opening. A number of elements are lost, including the postparietals, the tabulars, the supratemporals and intertemporals, and the postfrontals; a single element, generally interpreted as a prefrontal, in modern turtles fills the area originally occupied by that element and by the nasal and lacrimal as well. The cheek is rather puzzling in many respects. In many forms most of this region is bare of dermal bones. The hole so formed is not a true temporal opening, for it has no back rim of superficial dermal bone. Seemingly, there has been merely an eating-away of the skull roof from the

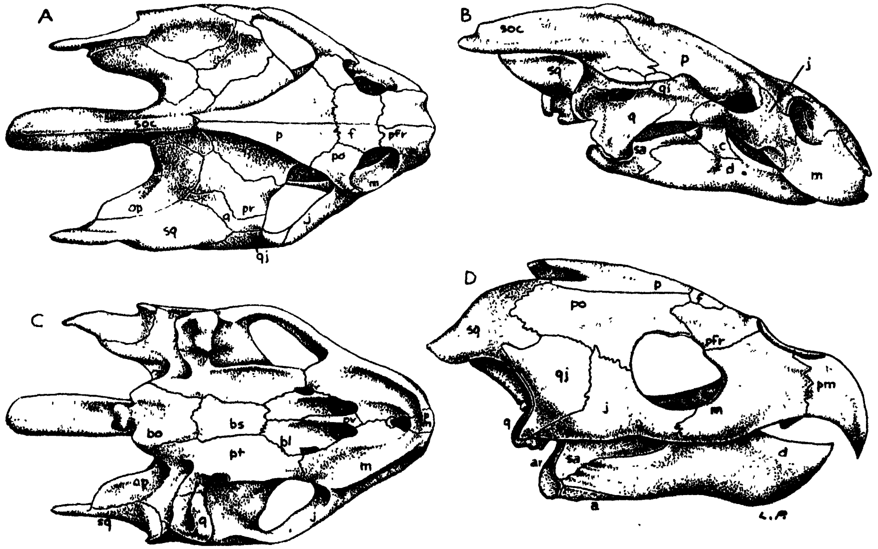


FIG. 139.—The skull in chelonians. *A*, Dorsal; *B*, lateral; and *C*, ventral, views of the skull of *Trionyx tritor*, an Eocene trionychid turtle, jaw restored from a related species; skull length about 6 inches. *D*, Lateral view of *Archelon*, a Cretaceous marine turtle, skull length about 2½ feet. *pfr*, Prefrontal. For other abbreviations see Figure 96. (*A-C* after Hay; *D* after Wieland.)

back. From this point of view the turtles are technically anapsid and to be associated with the cotylosaurs. It has been argued that this hole was once a true temporal opening and that its posterior margin later disappeared; but some living turtles have a solidly roofed skull, and so did the oldest-known fossils.

Primitive turtles.—The previous description has been based on the more normal turtles. The oldest forms are found in Triassic deposits; and here in such a form as *Triassochelys* we meet with types which were in some respects more primitive.

All the shell elements of later turtles were already present, and their arrangement was essentially that of later forms. In addition, several pairs of mesoplastra—intermediate plastral elements not found in the modern turtles of northern continents—were present. It is probable that the limbs could not be withdrawn, but some protection was afforded them by a series of scutes projecting beyond the normal marginal region. Head and tail, as well, were not capable of being retracted and were covered with spines. The limb girdles were rather primitive, particularly the shoulder girdle (Fig. 138, *A*). The clavicles and interclavicle were already incorporated into the plastron but show their original character clearly, and there was possibly even a small cleithrum. In most of these primitive forms the pelvis was fused to both carapace and plastron. In the skull (Fig. 140) nasals, lacrimals, and prefrontals are present and distinct; the temporal region was completely roofed, while the most striking feature of all is that, although a horny beak was apparently already developed, there were still tiny teeth on the palate.

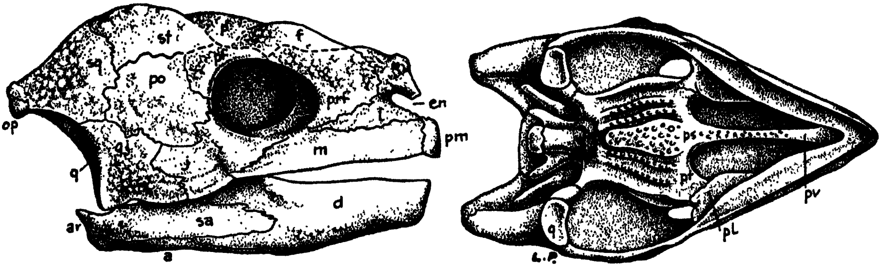


FIG. 140.—The skull of *Triassochelys*, a primitive Triassic turtle still retaining teeth; lateral and ventral views. Length of original about $5\frac{1}{4}$ inches. For abbreviations see Figure 96. (After Jaekel.)

These Triassic forms were primitive representatives of the oldest group of turtles, the suborder Amphichelydia, which included the dominant forms in the Mesozoic. There were a number of families, which differed in many respects. Teeth were unknown except in *Triassochelys;* the later forms were more modern in certain aspects, and some appear to be transitional to the later pleurodires and cryptodires, while retaining a number of archaic features. One or two amphichelydians lingered in the Eocene of North America. Apart from this, the only late survivors of the group appear to be some large forms in the Southern Hemisphere, with peculiarly horned skulls, of which *Meiolania* of the Australian Pleistocene is the last representative; the remains are incomplete, but some idea of its size may be gathered from the fact that the skull was 2 feet broad.

Pleurodires.—Most direct descendants of these archaic chelonians are the members of the suborder Pleurodira, the "side-neck" turtles. The distinguishing feature of the Mesozoic types included in the previous suborder was the impossibility (as shown by the structure of the neck vertebrae) of drawing the head into the shelter of the shell. This has been accomplished in the pleurodires; but, in contrast with most living turtles, the head is withdrawn by a sideways bending of the neck. Nasals and lacrimals are lost, as in cryptodires, but in contrast is the fusion of the pelvic girdle to the shell. A number of primitive features still persist, such as the presence of mesoplastra in many forms. The oldest forms surely assignable to the pleurodires are from the Upper Cretaceous. Some pleurodires were then present in the Northern Hemisphere, and a few remained in Eurasia and North America well into the Tertiary. Today they are confined to the three southern continents, as an example, repeated in many other groups, of the late survival in the tropics of archaic types.

Cryptodires.—More progressive and successful has been the suborder Cryptodira, in whose members the head is withdrawn straight back into the shell by means of an S-shaped curvature of the neck vertebrae. Mesoplastra are never present, nor is the pelvis ever attached to the shell. Types intermediate between the amphichelydians and the cryptodires appeared in the Jurassic; in the early Cretaceous typical cryptodires appeared and have since become the dominant types in northern areas and have invaded the seas as well.

The generalized stock of the cryptodires seems to lie among the marsh turtles and terrapins of the families Dermatemydidae and Emydidae. These are amphibious forms, moderately flattened as to body and with a complete, well-ossified carapace and plastron. Turtles of this sort appeared in the Lower Cretaceous and are common in many Tertiary deposits; *Stylemys*, for example, is an extremely abundant fossil in the White River Oligocene. The tortoises—*Testudo* (Fig. 137) and its relatives—are the one group of chelonians which are truly terrestrial in habits and, apart from technical features, are readily distinguished by their highly arched and well-ossified shells. The tortoises are found throughout the Tertiary. A number of species of large size are found today on various isolated islands where the absence of land enemies has afforded them even more protection than that which is given them by the shell; some fossil tortoises were equally large, notably one from the late Pliocene of India, which is often referred to as a separate genus, *Colossochelys.* A variant from amphibious life toward a fully aquatic one is seen in *Chelydra* and related snapping turtles, somewhat aberrant American river dwellers, which are known from various Tertiary localities.

Full aquatic adaptations have been attained by a series of marine turtles. A number of such types appeared in the Cretaceous, and a few are present in the oceans today. Of the extinct forms the best-known are *Protostega* and the related *Archelon* (Fig. 139, *D;* 141) of the Cretaceous. These old sea turtles were large types, up to a dozen feet in length. Land turtles seldom grow to any great size; but in the water, of course, many of the problems of support do not arise. The heavy armor of a turtle, however, means a much-increased specific gravity and a consequent expenditure of energy in maintaining the body in the water; it would be highly advantageous if the armor were lightened and the weight consequently reduced. This was rendered possible by the fact that in taking to the sea many land enemies were left behind, and for a large form there were few or no marine enemies; it was consequently possible for a marine turtle secondarily to reduce its armor to a considerable extent, leaving a small amount of bony framework.

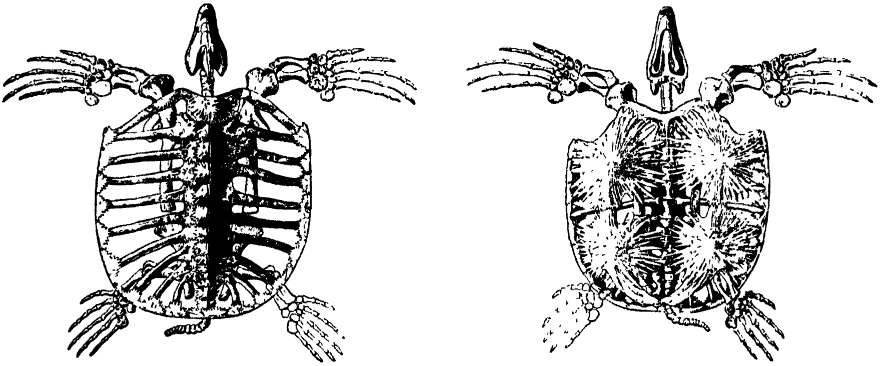


FIG. 141.—*Archelon,* a Cretaceous marine turtle, dorsal and ventral views. Original about 12 feet long. (From Wieland.)

The compact shape of a turtle's body and the small size of the tail renders swimming by a fishlike movement out of the question. Consequently, it was necessary for the feet to develop into powerful swimming paddles, by which the turtle might row itself through the water. The proximal part of the limbs of these oceanic forms is short but powerful, while the fingers are elongated and broadened to form large, webbed flippers.

Of a number of such turtle types which evolved in the Cretaceous, most are extinct; but *Chelonia* [*Chelone*] and a few related forms have survived to modern times. This living genus is, in general, still similar in build to the oldest forms.

A second marine type is *Dermochelys*, the leathery turtle. In this form there is almost no connected dermal skeleton at all, merely a series of small bony plates studded in the skin of the back. It has been argued that this really represents the primitive chelonian condition and that the leathery turtle is the most primitive known member of the entire order. But there is no fossil evidence to substantiate this, for the complete development of the armor had taken place by the Triassic; and, of the few imperfect fossils which appear to represent relatives of *Dermochelys*, none is earlier than the Eocene. We have just seen that other marine turtles tend to reduce their armaments; and it is probable that *Dermochelys* is merely a marine type in which reduction has gone much further than is usually the case.

These oceanic turtles are the first examples that we have encountered of reptiles returning to a marine existence. Later, however, we see further examples of this type of adaptation in other reptilian groups.

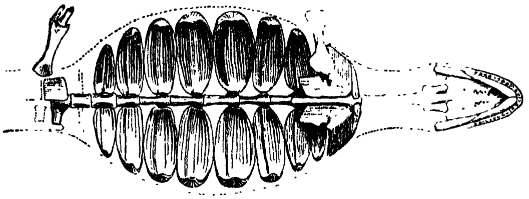


FIG. 142.—Ventral view of *Eunotosaurus*, a small Permian reptile possibly ancestral to the chelonians, about $\frac{2}{3}$ natural size. (From Watson.)

Trionyx, the living soft-shelled turtle, is a river-dwelling type with a very flat body in which the armor is somewhat reduced and on which horny scutes are entirely lacking, the plates being covered only with a leathery skin. Sometimes placed in a separate suborder, these turtles are perhaps also to be regarded merely as aberrant cryptodires. Related types had developed by the Cretaceous, very probably from relatives of the snapping turtles. *Trionyx* (Fig. 139, *A–C*) is a common fossil form.

Turtle origins.—But little light is shed on the ultimate origin of the turtles from a study of fossil members of the order. Some early Triassic forms, such as *Triassochelys*, show a structure slightly more primitive than that of most later turtles. But even at that time the armor was nearly perfectly developed; we are dealing definitely with a true turtle and not with a transitional type. The ancestors of the group must be sought farther back—in Permian times.

A possible connecting form is *Eunotosaurus* (Fig. 142), a small reptile from the Middle Permian of South Africa. Unfortunately, the roof of the skull is unknown; we cannot settle the problem of the presence or absence of a temporal opening. Teeth were still present. The limbs, too, are poorly known, but the girdles appear to have been of a primitive character. The greatest point of interest lies in the skeleton of the trunk. There was only a small number of vertebrae, a fact suggesting the reduction which has taken place in turtles. Especially significant seems to be the fact that following the small first rib were eight exceedingly broad ribs which extended far laterally and almost touched one another at their edges. This may be compared with the condition in turtles in which there are eight ribs supporting the costal plates which make up the most of the carapace. There is one marked difference; for in *Eunotosaurus* the plates were an expansion of the rib itself, while in turtles there is a separate dermal ossification. But it is not improbable that this form was closely related to the turtle ancestry, and the development of separate plates may have been preceded by the stage seen here. This creature was not, of course, a true turtle; on the other hand, it was far from the typical cotylosaurs. Perhaps we may include it in the Chelonia in a broad sense but place it in a separate suborder, the Eunotosauria.

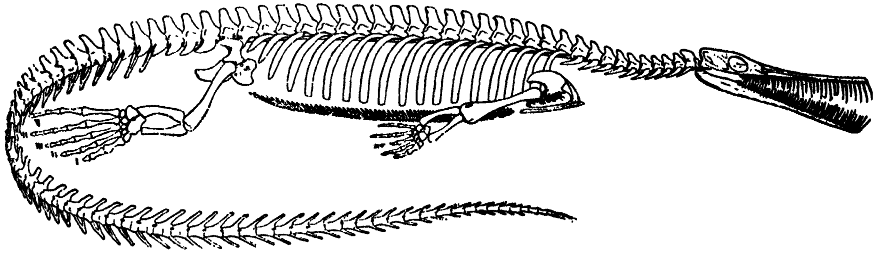


FIG. 143.—The skeleton of *Mesosaurus*, a late Carboniferous or early Permian aquatic reptile from the Southern Hemisphere; length of original about 16 inches. (After McGregor.)

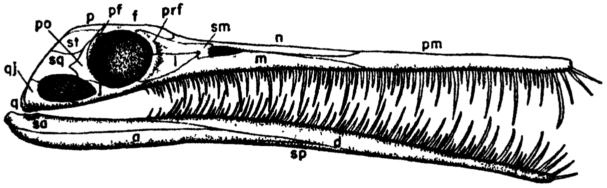


FIG. 144.—The skull of *Mesosaurus*, about natural size. For abbreviations see Figure 96. (After von Huene.)

Mesosaurs.—While reptiles originated as land forms, many groups took again to water. Earliest of all aquatic types were *Mesosaurus* (Figs. 143, 144) and its allies, constituting the Mesosauria (or Proganosauria). These were slimly built little reptiles about a yard in length, which apparently were active, fish-eating forms, inhabiting bodies of fresh water. Their remains are known only from deposits in South Africa and South America, which appear to be of late Carboniferous or early Permian age. This distribution has been used as an argument for the former union of those continents. But it may merely mean that they lived in an environment other than that of the coal-swamp pools from which specimens of contemporary vertebrates have been recovered in Europe and America and may possibly have been widely distributed.

The mesosaur skull was long and slim, the neck and body elongate, and there was a long, powerful, laterally compressed tail. The last seems to have been the principal swimming organ. But, while the front legs were not particularly long and presumably functioned merely as steering organs, the hind legs were long and strong, suggesting that they also were of considerable use in locomotion.

The vertebrae were of a primitive type with broad arches like those of cotylosaurs. The dorsal ribs (which attached by a single head to the transverse processes) were curiously thickened, rather banana-like; a similar structure is found in some marine sirenians among mammals, and this "pachyostosis," it is suggested, is due to some physiological change connected with aquatic life.

The shoulder girdle had the usual reptilian elements—a single coracoid and a scapula, a clavicle and an interclavicle. As was general in aquatic forms, the scapula was short and broad, the coracoid large. The pelvis was rather primitive but was partly unossified. The limbs were not much modified for aquatic life; the long bones were little shortened. Presumably, the spreading digits of the feet were webbed. In the toes of such marine forms as the ichthyosaurs and plesiosaurs there was a tendency for increase in the number of joints. Here, however, the phalangeal formula was normal except for an extra joint or two in the fifth toe in the pes.

There was a long, slender, fish-eating type of snout; the nostrils were pushed far back—an aquatic adaptation for easier breathing; the teeth were very long and sharp and set close together; the tooth-bearing palate is derivable from the generalized type seen in most primitive reptiles. The temporal region was long unknown; recent studies indicate that there was a single large lateral opening.

The very early appearance of this group suggests that they were an extremely early offshoot of the stem reptiles, the cotylosaurs. They do not appear in typical Permian deposits and hence had a very short span of life. It has been suggested that they were ancestral to the ichthyosaurs. But common features are merely such as might (and did) occur in other aquatic reptiles; the ichthyosaur hind legs are reduced, not enlarged, and the temporal region is very differently constructed. The lateral temporal opening suggests inclusion of the mesosaurs in the synapsids, or mammal-like reptiles. No other features of mesosaurs, however, show any resemblance to that group, and it is probable that the mesosaurs are an independent and early side branch from the Carboniferous stem reptiles.

Ichthyosaurs.—Of all reptiles, those most highly adapted to an aquatic existence were the ichthyosaurs, which well deserve their name of "fish reptiles." They seem to have occupied the place in nature now taken by the dolphins and porpoises. They were particularly numerous in the Jurassic, but their life-span seems to have covered the greater part of the Mesozoic.

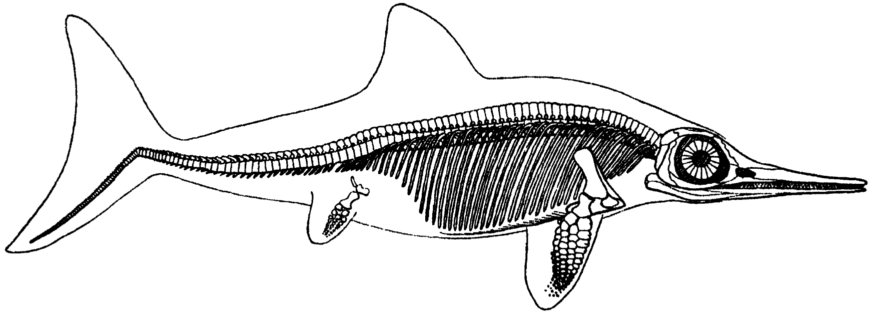


FIG. 145.—A Jurassic ichthyosaur, much reduced. (Simplified from E. von Stromer.)

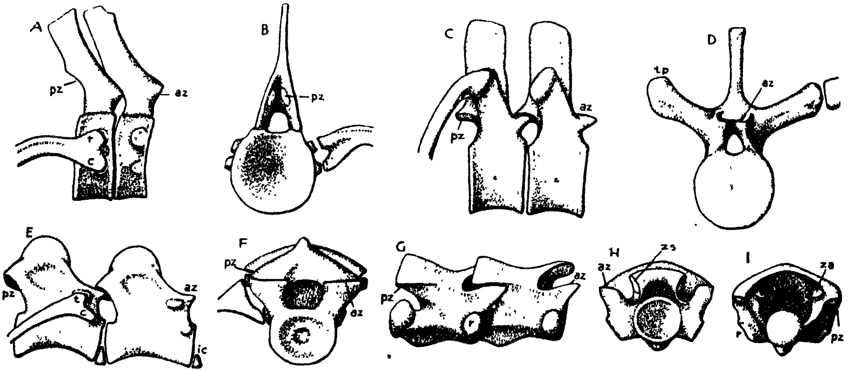


FIG. 146.—Dorsal vertebrae of various reptiles. *A*, *B*, Lateral and posterior views of vertebrae of the ichthyosaur *Ophthalmosaurus*; *C*, *D*, lateral and anterior views of vertebrae of the plesiosaur *Cryptocleidus*; *E*, *F*, lateral and anterior views of vertebrae of the protorosaur *Araeoscelis*; *G*, *H*, *I*, lateral, anterior, and posterior views of vertebrae of the Cretaceous snake *Coniophis*. Abbreviations: *az*, anterior zygapophysis; *c*, capitulum of rib; *ic*, intercentrum; *pz*, posterior zygapophysis; *r*, rib articulation on centrum in squamata; *t*, tubercule of rib; *tp*, transverse process of neural arch; *za*, *zs*, zygantrum and zygosphene, additional articular processes of neural arch. (*A–D* after Andrews; *E*, *F* after Williston; *G–I* after Marsh.)

The typical Jurassic forms (Fig. 145) seem to have been very fishlike in their superficial appearance. There was a large, fishlike caudal fin. The body was short and deeply fusiform and apparently somewhat compressed laterally. Perfectly preserved specimens show the body outline and reveal the presence of a large dorsal fin, unsupported by bone. The limbs were reduced (especially the pelvic ones) to short steering paddles, the main swimming motion being a fishlike undulation of the body and the tail fin. The vertebral centra (Fig. 146, *A*, *B*) were short amphicoelous disks to which attached both heads of the two-headed ribs. The caudal series of vertebrae appear to be broken in fossil specimens, with the tip of the tail bent downward. This was once thought to be a post-mortem effect, and the tail was restored as a straight structure. But we now know that this seeming break was natural and that ichthyosaurs had developed a reversed, but otherwise sharklike, heterocercal tail fin (Fig. 149).

All the bones of the girdles were present but none too well ossified; and the elements were small, especially the dorsal ones. The pelvis had lost its connection with the sacral vertebrae. The long bones of the limbs were much shortened and, except for the humerus and femur, tended to become hexagonal or circular disks, as did all the more distal limb elements (Fig. 147, *B*). The paddle seems to have moved as a unit, flexible in structure but without any great motility between individual bones. There was always considerable hyperphalangy, or addition of extra finger joints, as in many marine forms. In addition, the number of toes varied; in some cases there was a decrease to three, in others hyperdactyly, with as many as seven or eight digits; sometimes a single toe is observed to divide into two, part way down the paddle.

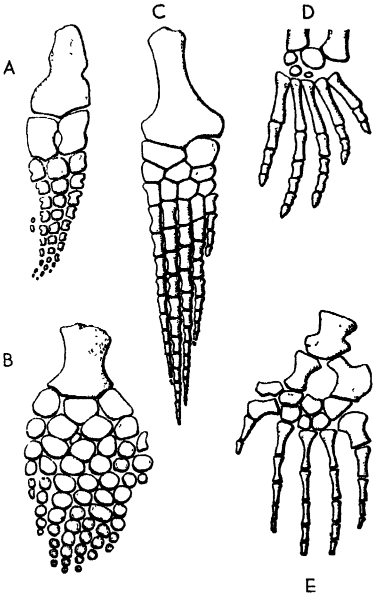


FIG. 147.—Limbs of various aquatic reptiles. *A*, Pectoral limb of the Triassic ichthyosaur *Merriamia; B*, same of the Jurassic *Ophthalmosaurus; C*, same of the Cretaceous plesiosaur *Elasmosaurus; D*, pes of the nothosaur *Lariosaurus; E*, pectoral limb of the mosasaur *Clidastes*. (*A* after Merriam; *B*–*E* after Williston.)

The skull (Fig. 148) was, of course, highly modified for aquatic life. The beak was long; the external nostrils had moved far back; the eyes were very large, with well-developed sclerotic plates; a pineal opening was present. With the enormous enlargement of the eyes, the temporal region had become much shortened. There was a large temporal opening, which lay high on the skull at either side of the parietals and was thus an upper temporal fenestra.

But, in contrast with other reptiles, its lateral border was formed by the postfrontal and supratemporal bones; the postorbital and squamosal elements lay farther down the cheek region and did not enter into its borders. The stapes, usually slim in reptiles, had a massive structure, suggesting that these types had undergone considerable change in their mode of hearing, as have the whales and other secondarily aquatic forms.

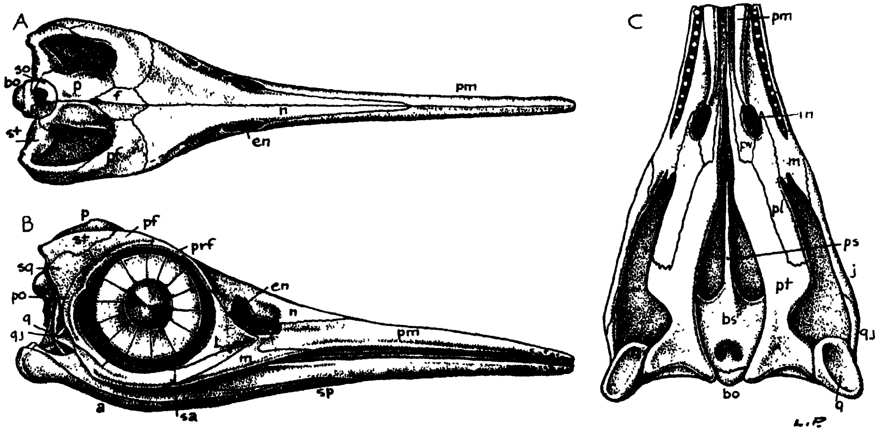


FIG. 148.—The ichthyosaur skull. *A*, *B*, Dorsal and lateral views of the skull of *Ophthalmosaurus*, skull length about 40 inches; *C*, posterior portion of palate of *Stenopterygius*. For abbreviations see Figure 96. (*A*, *B* after Gilmore; *C* from Abel after Owen and Smith Woodward.)

These creatures were extreme in their marine adaptations, and their limbs were obviously unfitted for use on land. It was long ago suggested that reproduction must have taken place in the water (in many snakes, for example, and in lizards, the eggs are retained in the mother's body until they are hatched). In agreement with the idea that the young were born alive are specimens which actually show skeletons of young ichthyosaurs inside the body of a large individual. It has been argued that these may have been youngsters which had been eaten by mistake. But recently several specimens have shown the young partially emergent from what would have been the cloacal region in life. The mother here apparently died during childbirth, or (there are human parallels) labor may have taken place after the death of the mother.

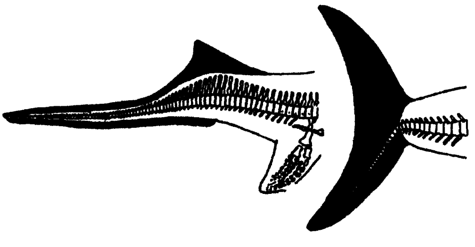


FIG. 149.—Tails of *Mixosaurus* (Triassic) and a Jurassic ichthyosaur, to show development of sharklike tail. (From Williston, after Wiman.)

The description above is that of a typical Jurassic form. The typical Triassic forms, such as *Mixosaurus*, were more primitive. The tail (Fig. 149) was much straighter, with little development of the fish type of caudal fin; the limbs were somewhat less specialized (Fig. 147, *A*); the face shorter.

These forms are found in marine Triassic beds of California and Spitzbergen. From these same deposits come fragmentary remains of *Omphalosaurus*, which represented a short-lived, shell-eating side branch of the group. The skull was, in sharp contrast with that of ordinary ichthyosaurs, short and strongly built, with flattened, button-like teeth for crushing mollusks. These forms seem to have paralleled the contemporary placodonts discussed later; like them they did not persist beyond the Triassic.

Most of the later ichthyosaurs have usually been included in a single genus, *Ichthyosaurus*. There were, however, a number of distinct types—deep-bodied and slender forms, broad-finned (*Eurypterygius*) and narrow-finned (*Stenopterygius*) series; and there was one ichthyosaur, *Eurhinosaurus*, with a short lower and long upper jaw like those of a swordfish.

In the Cretaceous the ichthyosaurs became rarer; they are quite unknown in the very well-known Upper Cretaceous fauna of the Kansas chalk, where plesiosaurs and mosasaurs abound, and they seem to have become extinct well before the close of the period.

Although the Triassic forms of ichthyosaurs were slightly more primitive than their Jurassic descendants, they were already very highly specialized marine types. No earlier forms are known. The peculiarities of ichthyosaur structure would seemingly have required a long time for their development and hence a very early origin for the group, but no known Permian reptiles are at all suggestive of an ancestral position. Apart from the aquatic features of the skeleton, the odd type of temporal opening shows that the ichthyosaurs were far removed from any other reptile orders, even other forms with an upper temporal fenestra, and it seems likely that they arose independently from early stem reptiles. Provisionally, at least, we may regard them as the types of a distinct subclass termed the Ichthyopterygia.

CHAPTER 9

SYNAPTOSAURIAN REPTILES

TREATED in the present chapter is a series of reptilian groups now entirely extinct but not uncommon in Permian and Mesozoic deposits. They were, in the main, amphibious or aquatic forms, of a highly diversified nature but showing a common diagnostic feature in the type of temporal opening present throughout. This opening was situated high up on the skull roof; it was essentially comparable to the superior temporal fenestra of diapsid types and was bounded below by a broad cheek plate. A similarly placed opening was, as we have seen, present in the ichthyosaurs. Here, however, the postorbital, squamosal, and parietal bones were the major elements forming its margins; the supratemporal, which plays a prominent role in the boundaries of the opening in ichthyosaurs, is absent. These forms may be considered as making up a subclass Synaptosauria; included are the various Permian and Triassic forms of the order Protorosauria and the order Sauropterygia—the nothosaurs, placodonts, and plesiosaurs of the Mesozoic seas.

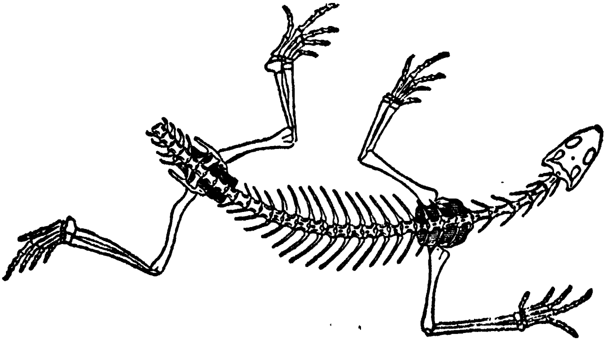


FIG. 150.—*Araeoscelis*, a small Lower Permian protorosaur, about ¼ natural size. (From Williston.)

Protorosaurs.—One of the few small Permian reptiles of which we have any adequate knowledge is *Araeoscelis* (Figs. 150, 151) of the Lower Permian beds of Texas. This was a small and lightly built creature little more than a foot in length, with very slender limbs; it may have appeared in life somewhat like one of the more agile lizards. The vertebrae (Fig. 146, *E, F*) were still amphicoelous as in primitive forms; the ribs, however, were much modified from the primitive condition. The cervical ribs were single-headed; those of the trunk were two-headed, but the capitular attachment had shifted upward to a point close to that of the tubercle, suggesting a transition to the single-headed condition seen in sauropterygians. Despite the slim build, there were still many primitive features in the limbs; the pubis and ischium, for example, formed a solid plate and lacked the large opening which developed there in many reptile types. The skull had retained many primitive features, particularly in the palate. But a small opening had developed high up in the side of the temporal region, bounded above by the parietal, behind by a small bone which may be either supratemporal or tabular, and below by the postorbital and squamosal. This last element was very large and occupied almost the entire surface of the broad cheek region, and the quadratojugal seems to have disappeared.

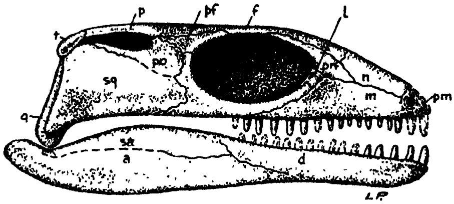


FIG. 151.—Lateral view of the skull of *Araeoscelis*; length of original about $1\frac{3}{4}$ inches. (The element labeled "tabular" is not improbably the supratemporal.) For abbreviations see Figure 96. (After Williston.)

This little form is quite different from its better-known large contemporaries. With it have been associated, with various degrees of probability, other rare reptilian types of the Permian and Triassic. These vary highly in many characteristics and are difficult to distinguish from contemporary two-arched reptiles, discussed later in this chapter. Where sufficiently known, however, they show certain basic features described in *Araeoscelis*—a single, upper, temporal opening; slim, single-headed cervical ribs; and dorsal ribs in which the two heads tend to unite to a single one situated on or close to the transverse process. In other respects there is much variation, but all may be provisionally grouped within a single order—the Protorosauria.

A few close relatives of *Araeoscelis* are known from Lower Permian deposits, and further types are known from the Upper Permian. *Protorosaurus*, as far as known, was similar to *Araeoscelis* but was a larger reptile, reaching a length of several yards. *Weigeltisaurus* [*Palaeochamaeleo*] is a persistently small form, but peculiar in the development of a spiked, bony frill at the back of the skull, resembling that of the (unrelated) modern chameleons. Other varied types were present in the Triassic. *Trilophosaurus* of the late Triassic of North America (Fig. 152) was a stoutly built reptile which superficially gives the impression of a cross between a diadectid cotylosaur and a rhynchocephalian diapsid. The short, deep skull has a toothless and presumably horn-covered beak, as in the rhynchosaurs described later; the cheek teeth were transversely widened and three-cusped, looking much like those of *Diadectes;* and the general proportions of the skull are suggestive of that cotylosaur. But the temporal opening, rib attachments, and other features are those diagnostic of the present group.

Radically different was *Tanystropheus* (Fig. 153) of the European Middle Triassic, a grotesque type whose mode of life is difficult to imagine. The greatest peculiarity is the extreme elongation of the neck vertebrae. The contrast between the cervical region and the stubby body and rather normal limbs is so extreme that, when a complete skeleton was found for the first time, it proved that the front part of the animal had been described by earlier writers as pertaining to a flying reptile, while the trunk had been thought to be that of a primitive dinosaur!

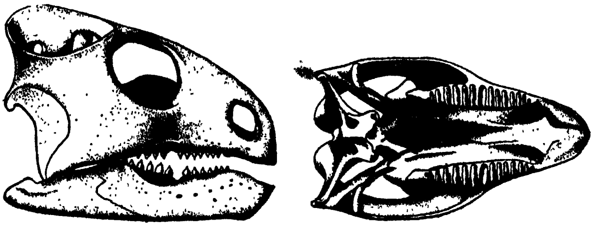


FIG. 152.—Lateral and ventral views of *Trilophosaurus*, an Upper Triassic protorosaur; length about 5 inches. (After J. T. Gregory.)

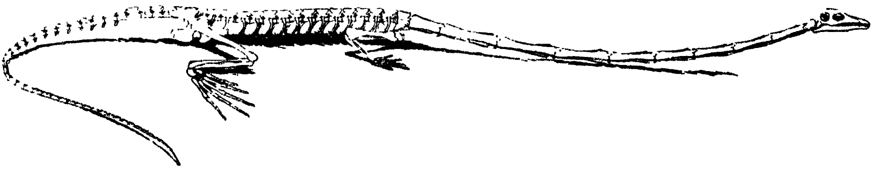


FIG. 153.—*Tanystropheus*, a long-necked Triassic protorosaur, about 2½ feet long. (From Peyer.)

A puzzling genus which may be mentioned here is *Pleurosaurus* (Fig. 154), an aquatic Upper Jurassic reptile. This was a very elongate, slender animal, a yard or two in length, with trunk and tail proportions comparable to those of a snake, except that small but normally built limbs were present. The teeth were acrodont, as in rhynchocephalians and some lizards; the temporal region had a single upper opening, bounded laterally by a broad bar, a situation suggesting that *Pleurosaurus* may be a late surviving protorosaur.

The protorosaurs seem to have been an early offshoot of the cotylosaurs, as attested by the fact that they were among the very few reptilian orders represented in early Permian deposits. Our knowledge of their evolution is still very incomplete, but they appear to have deployed rapidly into a number of varied lines. By the Triassic, however, they were in competition with various types of diapsid reptiles and seem to have been unable to meet this competition successfully, with resulting reduction in numbers and final extinction. It seems probable, however, that the sauropterygians, discussed below, are aquatic types descended from a protorosaur stock.

It is improbable that any other groups of reptiles are protorosaur descendants. It has been suggested that lizards, which also have a single upper temporal opening, were derived from such a form as *Araeoscelis*. Current belief, however, is that lizards are derived from diapsid ancestors. Again, it is theoretically possible to derive such diapsid forms from a protorosaur by the formation of a lateral opening below the upper fenestra already present; the available evidence, however, suggests that the two-arched reptiles were of independent origin.

Sauropterygians.—The plesiosaurs, one of the most important of marine reptilian types, may be included with related Triassic forms, such as the nothosaurs and placodonts, in an order Sauropterygia.

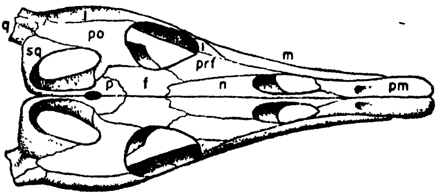


FIG. 154.—*Pleurosaurus*, an aquatic Jurassic reptile of doubtful affinities, skull length about 4 inches. (After Broili and Watson.)

In all these reptiles, aquatic adaptations were developed, and, in addition, there were a number of common structural features which tend to show their mutual relationship. There was a single upper temporal opening which, as in *Araeoscelis*, lay above a broad cheek plate formed mainly by the squamosal, while the quadratojugal was absent. The pineal eye had been retained, while the nostrils had, as in many marine forms, moved well back along the top of the skull. There was no secondary palate, but the interpterygoid vacuities were nearly or entirely closed by a fusion of the pterygoids in the midline below the old roof of the mouth. The vertebrae (Fig. 146, *C*, *D*) were rather primitive in build, amphicoelous or, at the most, flat-ended. The ribs of the trunk region had but a single head which articulated with the transverse process of the neural arch rather than the centrum. The old ventral-rib system had (as in *Araeoscelis*) been retained and powerfully developed to form a basket-like structure along the belly.

The limbs and girdles were usually considerably modified for aquatic life. The dorsal elements of the girdles (scapula, ilium) were reduced in size; the ventral ones tended to be expanded. The sacral articulation was reduced in relation to the lessened need of support as terrestrial life was abandoned. The limbs of the nothosaurs and placodonts were still more or less primitive and not ill suited to walking as well as swimming; in the plesiosaurs they were long, paddle-like structures.

Plesiosaurs.—The plesiosaurs are the best-known members of the sauropterygians, as well as the last to survive and the most specialized for aquatic life; they are common in many Jurassic and Cretaceous deposits. Many of them were of considerable size, with a maximum length of about 50 feet. Although they were obviously well fitted for marine life, their adaptations were very different from those of the rival ichthyosaurs. The latter swam by a fishlike undulation of the body and tail, the fins were merely for steering, and the head did not move independently of the body as a whole. In the plesiosaurs, however, the body (Figs. 155, 156) was broad and flat, and the tail seems to have been of comparatively small importance; swimming seems to have been accomplished through rowing the body along by means of the well-developed paddles. The head, usually small, was set on the end of

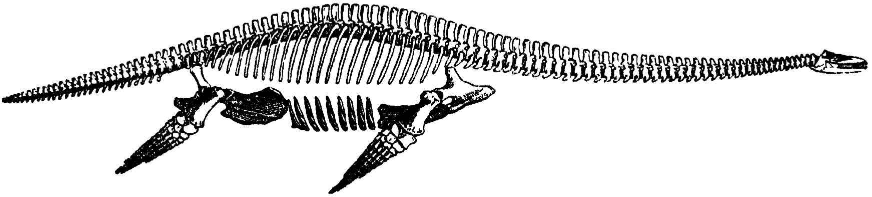


FIG. 155.—*Muraenosaurus*, a long-necked Jurassic plesiosaur, about 21 feet in length. (From Andrews.)

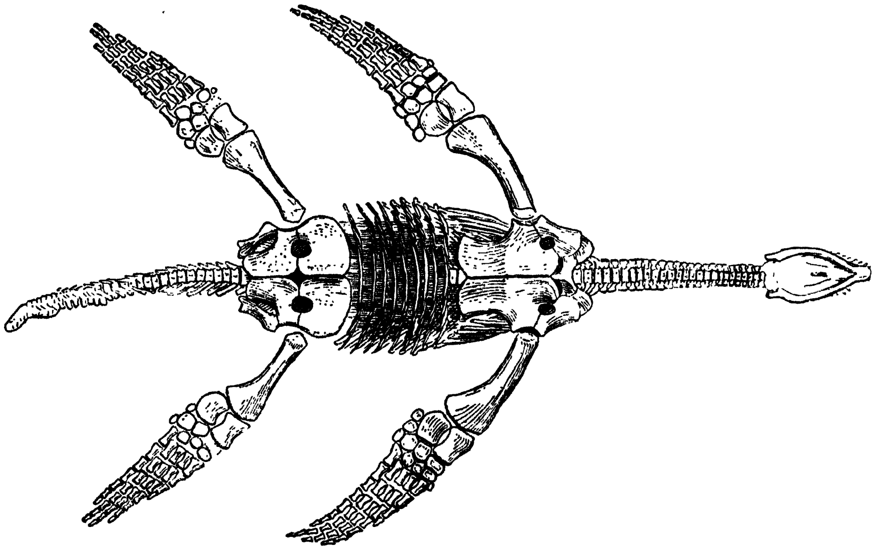


FIG. 156.—*Thaumatosaurus*, a Jurassic plesiosaur, ventral view, to show the abdominal ribs and expanded girdles, about 11 feet long. (After Williston, adapted from Fraas.)

a flexible neck and could dart sidewise to seize the prey. A plesiosaur has been compared by an old writer to "a snake strung through the body of a turtle."

The skull (Fig. 157) was variable in shape, most forms having a short face, while in others shortness of the neck was compensated by an elongated beak. The external nares had been pushed back to a position comparable to that found in ichthyosaurs. The palate was highly modified; the two pterygoids met each other beneath the basisphenoid, separated to disclose a small interpterygoid vacuity, and then met again farther forward. The pointed teeth, set in sockets, were confined to the margin of the jaws.

The scapula (Fig. 158, above) had only a small dorsal blade, but ventrally it and the coracoid had expanded into a huge ventral plate for the attachment of strong muscles which gave a powerful down-and-back stroke to the paddle. In the pelvic girdle (Fig. 158, below) the ilium was very short and but loosely attached to the tip of the sacral ribs. The pubis and ischium, however, had developed to form a very large plate containing a small vacuity.

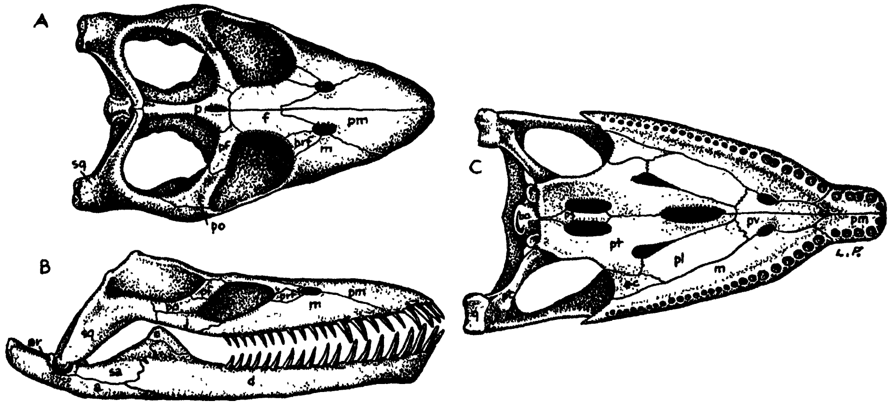


FIG. 157.—The skull in plesiosaurs. *A*, Dorsal view of skull of *Muraenosaurus*; *B*, lateral view of same, skull length about 14 inches; *C*, palatal view of *Thaumatosaurus*, skull length about 14 inches. For abbreviations see Figure 96. (*A*, *B* after Andrews; *C* after Fraas.)

The humerus and femur were long, while the bones of the distal segment of the limb were much shortened. The paddles (Fig. 148, *C*) were very long but less specialized than the fins of the ichthyosaurs; for, although there was considerable hyperphalangy, there was never any hyperdactyly, and the phalanges retained the shape of normal finger joints.

Plesiosaurs first appear in the Rhaetic deposits, laid down at a time transitional from the Triassic to the Jurassic. In the marine Liassic deposits of the Lower Jurassic of Europe the group was already abundant and diversified. Two types, quite different in adaptive features, are early apparent. *Plesio-*

saurus and *Muraenosaurus* (Figs. 155, 157) are representative of a group with small, short heads; an elongate neck; and short proximal bones in the limb paddles. *Pliosaurus* and *Thaumatosaurus* (Figs. 156, 157) are, on the other hand, types which had a relatively short neck but tended to increase the length of the head in compensatory fashion; humerus and femur tended to be more elongate than in the long-necked genera. The pliosaurs tended, even in the Jurassic, to become large forms; and a late representative—*Kronosaurus* of the Australian Lower Cretaceous—had a skull nearly 3 yards in length.

Jurassic plesiosaurs are mainly from European deposits; a second major fauna is that of the last appearance of the group, in the late Cretaceous, mainly known from specimens from western North America. All Upper Cretaceous genera show specializations in the union of the two heads of the cervical ribs into a single structure and a shortening of the elements of the second segment of the limbs. Long- and short-necked groups, however, persisted. The long-necked forms are the more numerous and include such genera as *Elasmosaurus*, with seventy-six vertebrae in its flexible neck. The short-necked forms have a modest cervical count—thirteen, for example, in *Brachauchenius*.

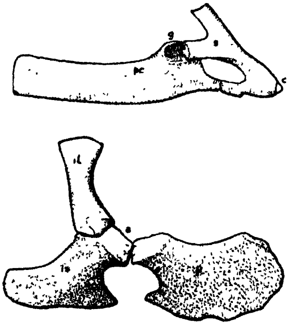


FIG. 158.—*Above*, shoulder girdle of the plesiosaur *Microcleidus*. The scapula has grown downward and backward to gain a ventral contact with the coracoid. *Below*, pelvis of *Muraenosaurus*. Abbreviations: *a*, acetabulum; *c*, clavicle; *g*, glenoid; *il*, ilium; *is*, ischium; *p*, pubis; *pc*, precoracoid; *s*, scapula. (*A* after Watson; *B* after Andrews.)

Nothosaurs.—Much more primitive sauropterygians are present in the Triassic strata, particularly the marine beds of the Middle Triassic of Europe. *Nothosaurus*, *Simosaurus* (Fig. 159), *Ceresiosaurus* (Fig. 160), and a number of other genera of that age were types not yet completely adapted to aquatic life and, on the average, considerably smaller than the plesiosaurs. The general proportions of the body and the structure of the girdles were quite similar to those of the plesiosaurs. The limbs, however, were little specialized for aquatic life, except that the distal segments were somewhat shortened. The digits (Fig. 147, *D*) were of rather normal build but were probably webbed. In the skull the nostrils were "in transit" between the normal position and that found in plesiosaurs. The palate shows much the same general type of construction but was a quite solid structure, for the two pterygoids met in the mid-line for their entire length to form a continuous plate. In this respect the typical nothosaurs were already more specialized than the plesiosaurs and hence, despite the similarities in other respects, cannot have been plesiosaur ancestors.

A possible plesiosaur ancestor is *Pistosaurus* of the Middle Triassic. The skull, which alone is preserved, has usually been regarded as that of a nothosaur. Reinvestigation shows, however, that the palate is not completely closed; in this and other suggestive details of skull construction we find evidence of plesiosaur relationships.

The exact ancestry of the nothosaurs is uncertain. *Trachelosaurus* of the early Triassic of Europe is incompletely known but may be a terrestrial ancestor of the sauropterygians. As in this group, the neck was considerably elongated, containing about twenty vertebrae; the limbs, on the other hand, indicate that the genus was a land dweller.

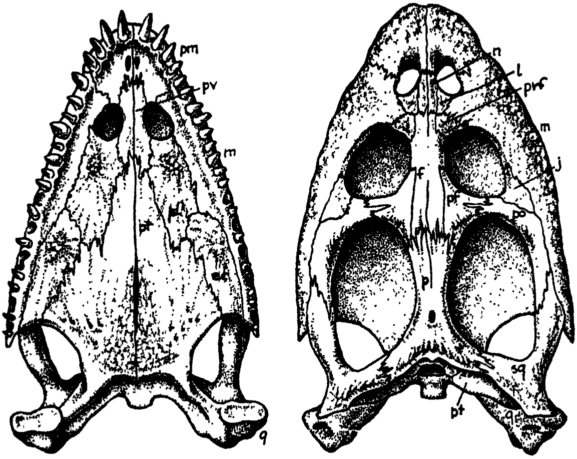


Fig. 159.—The skull of the nothosaur *Simosaurus*, dorsal and ventral views; length of original about 12 inches. For abbreviations see Figure 96. (After Jaekel.)

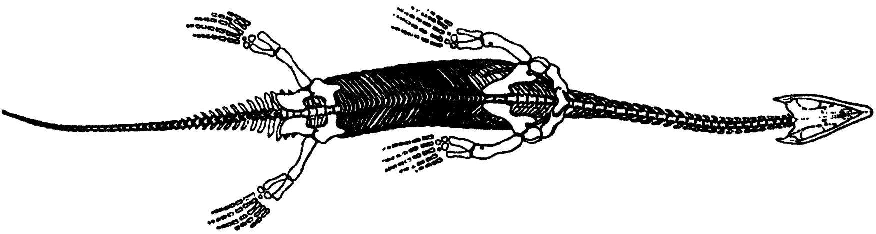


Fig. 160.—*Ceresiosaurus*, a Triassic nothosaur, ventral view; original about 3½ feet long. (From Peyer.)

Placodonts.—*Placodus* is the best-known member of a small group of aberrant Triassic sauropterygians which had taken up mollusk-eating as a livelihood. Connected with this is the most remarkable specialization of *Placodus* (Fig. 161), the development on the palate and lower jaws of enormous flat teeth capable of crushing mollusk shells. These teeth were not unlike those of some of the pavement-toothed sharks and, indeed, were long thought to pertain to fish. Presumably there were very powerful jaw muscles for this heavy work, for the coronoid bone of the jaw forms a long upwardly directed process for muscular insertion. This remarkable development simulates that found in mammals and is almost without parallel in ordinary reptilian types. The front teeth were heavy, projecting pegs across a broad muzzle in *Placodus* and may have served to root up mussels.

Apart from adaptations for this specialized diet, *Placodus* was not dissimilar to the nothosaurs in many features of limb and trunk structures; the skulls were essentially similar in such features as the position of the nostrils and the solid palate. However, the placodont trunk was relatively short and rounded in cross-section; and in the *Placodus* skull the tooth-bearing palatines have pushed back at the expense of the pterygoids. *Placodus* shows a further specialization in that numerous nodules of bone were found associated with the skeleton, indicating the beginning of body armor.

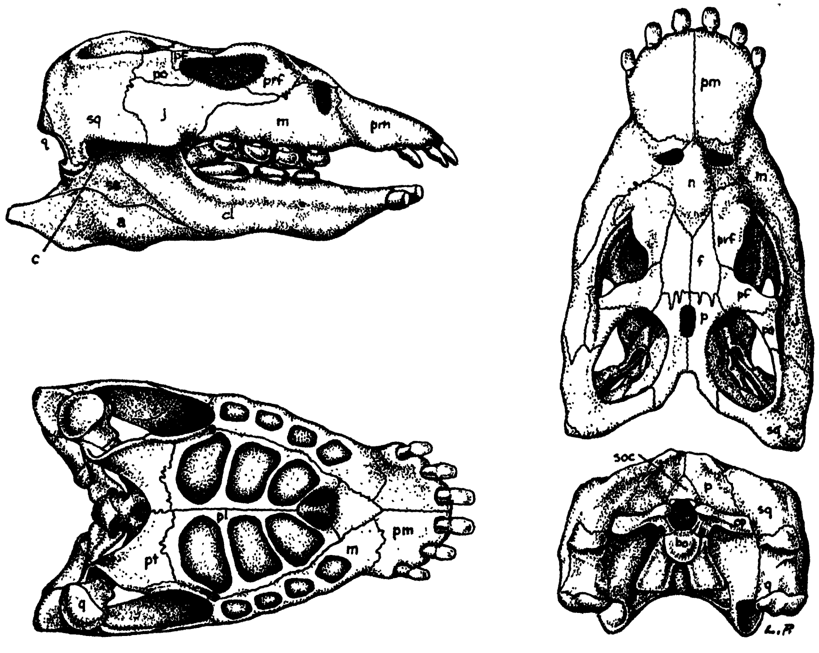


Fig. 161.—The skull of the placodont reptile *Placodus;* original about 10 inches long. For abbreviations see Figure 96. (After Broili.)

The *Placodus* specializations are intensified in other placodont genera of the middle and late Triassic of Europe. The crushing teeth may become larger but fewer in number; the snout may become slim and, in *Placochelys*

(Fig. 162), toothless, the sharp beak perhaps functioning as a pair of forceps in picking out mollusks; another genus, *Henodus*, became nearly completely toothless and presumably had developed stout horny plates, analogous to those of a turtle, for masticatory purposes. The more specialized placodonts developed the armor to a higher degree; and in *Henodus* and other genera the short, broad, and flattened body was completely incased in a shell comparable to that of the turtles. However, the placodont armor was composed of a much greater number of plates than in the Chelonia, arranged in a mosaic somewhat comparable to the carapaces of ankylosaur dinosaurs or glyptodont edentates.

It has been suggested that the placodonts were related to the turtles. Some sort of distant relationship of chelonians and sauropterygians is possible; we must note, however, that it is in the later and most highly specialized placodonts, not the more primitive ones, that the turtle-like features are most marked.

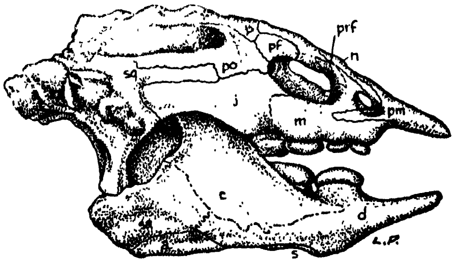


FIG. 162.—Lateral view of the skull of the placodont *Placochelys*; length of original about 6 inches. For abbreviations see Figure 96. (After Jaekel and von Huene.)

In the known sauropterygians we see, from the beginning of the Triassic on, a series of stages leading from terrestrial to purely marine reptiles, together with various side lines. Here, apparently, aquatic life was a much later specialization than in the ichthyosaurs, and the ancestors of the sauropterygians are presumably to be sought among the land animals of the Permian. As we have seen, *Araeoscelis* of that period is a land form which might well have been the ancestral type. While such a conclusion is, of course, to be regarded as a provisional one, we may be justified in associating the Protorosauria with the Sauropterygia in a common subclass, Synaptosauria.

CHAPTER 10

LEPIDOSAURIAN REPTILES

THE reptiles so far described have been either anapsids, with a solid skull roof, or forms with but a single temporal opening. However, except for marine types, the great bulk of Mesozoic reptiles were two-arched forms, with a temporal opening both above and below a bar formed by the postorbital and squamosal bones. This is the diapsid condition (cf. Fig. 132), and all forms with this double opening have often been grouped as members of a single subclass (the Diapsida). But many of the diapsids were advanced types showing evidences of close relationship to one another but not especially to more primitive, two-arched types. We prefer to regard the advanced forms—the crocodiles, dinosaurs, and pterosaurs—as members of a subclass Archosauria, which will be considered in later sections. In this chapter we shall treat only of some primitive, two-arched forms and types derived from them; these may be considered as constituting the subclass Lepidosauria, using a term frequently applied to the scaly reptiles (lizards, snakes, and *Sphenodon*) which are the modern representatives of the group.

Eosuchians.—No two-arched reptiles are known from the early Permian. First of such types to appear were a number of small reptiles from the Upper Permian of South Africa, of which *Youngina* (Fig. 163) is the best known. This form appears to have had a comparatively primitive postcranial skeleton, with moderately slender limbs, normal reptilian foot structure, and (as far as can be told) body proportions not unlike those of typical lizards.

In the skull were retained many primitive features which bring *Youngina* in contrast to the archosaurians to be described in the next chapter. The palate was of a very generalized reptilian type, with pterygoids movable on the braincase and with teeth on the palatal bones, in addition to a row of teeth set in sockets on the jaw margins. Small supratemporal, postparietal, and tabular bones were still present at the back of the skull, a pineal eye had been retained, and (unlike many archosaurs) there was no opening between the bones in the side of the slim snout.

Youngina, nevertheless, had two temporal openings—a lateral one far down the side of the cheek region, and a large upper opening on the top of the broad skull table. We are dealing with a diapsid reptile, but a very primitive one; and it seems fitting that *Youngina* and its few small and inadequately known relatives should constitute a separate order, the Eosuchia.

Apart from forms of such a seemingly primitive and unspecialized structure as that seen in *Youngina*, the order Eosuchia may be considered to embrace a number of other and varied early diapsid types. One such form is *Prolacerta* of the South African Lower Triassic (Fig. 164). In many respects this genus is similar to the earlier *Youngina* and may have been derived from it. But in the temporal region the lower bar is incomplete. This strongly suggests that the lizards, with an "open" cheek and a single temporal opening, have been derived from two-arched reptiles through loss of the lower arch.

A dubious group is that of the thalattosaurs (Fig. 165), rather small and poorly known aquatic reptiles from the marine Upper Triassic of California. The limbs of *Thalattosaurus* were paddle-like, but otherwise the postcranial skeleton is inadequately known. The skull was rather elongate, and sclerotic plates were present in the eyes. In the temporal region there was certainly a lower opening, but the presence or absence of an upper opening is uncertain owing to the fragmentary nature of the specimens. If diapsids, they may represent an offshoot of the eosuchian stock.

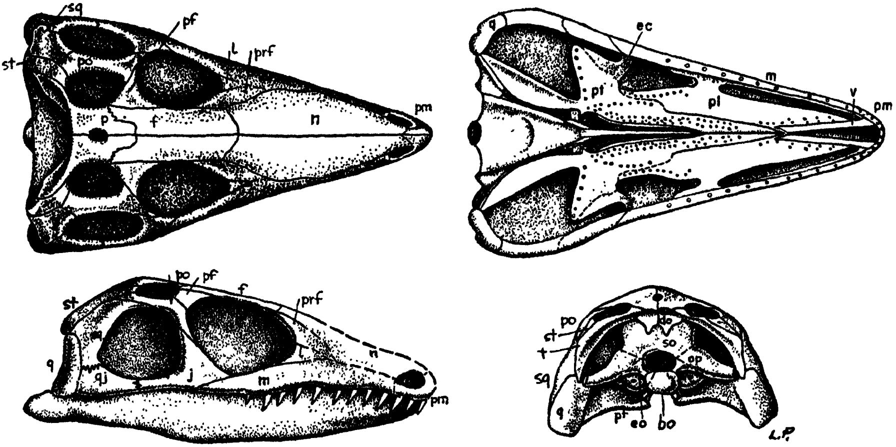


FIG. 163.—*Youngina*, a primitive, two-arched reptile from the Upper Permian of South Africa—dorsal, palatal, lateral, and occipital views; length of original about 2½ inches. For abbreviations see Figure 96. (After Broom, Watson, Olson.)

Champsosaurus (Fig. 165) is a reptile found in late Cretaceous and early Tertiary deposits in both Europe and North America, which appears to have been a fish-eating dweller in fresh waters. In its general proportions it gives the appearance of a small crocodilian, and its long-snouted skull is superficially comparable to that of a gavial. The external nostrils were at the tip of the long snout; the internal nares were carried far back, although there was no development of a true secondary palate. Although *Champsosaurus* was a diapsid, it is not at all closely related to the crocodiles. It is frequently included in the Rhynchocephalia, but it lacks the rhynchocephalian beak, and the teeth are socketed rather than acrodont; hence it seems best to regard it as a specialized late survivor of the eosuchian group of primitive diapsids.

Rhynchocephalians.—Still primitive in many features, but with a few characteristic specializations which mark them as an aberrant group, are the Rhynchocephalia, which first appeared in the Triassic and survive in the shape of a small reptile, *Sphenodon*, inhabiting a few islands off the coast of New Zealand. *Sphenodon* (Fig. 166) looks very much like a lizard and, indeed, resembles the lizards greatly in many features; while, on the other hand, it appears, in the retention of numerous primitive characters, to have departed little from the structure of the Eosuchia. It is sharply marked off from the lizards, in which the cheek is bare beneath the upper opening and bar, by the presence of two temporal openings. It is easily distinguished from the eosuchians by two specialized features: the teeth are fused to the edge of the jaws rather than set in sockets (acrodont), and there is a small overhanging beak on the upper jaw, a characteristic to which the group name refers.

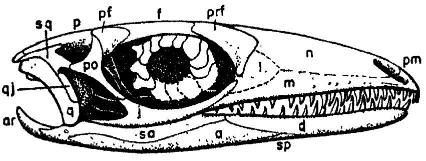


FIG. 164.—*Prolacerta*, an eosuchian, seemingly ancestral to lizards; length of skull about 2½ inches. For abbreviations see Figure 96. (After Camp.)

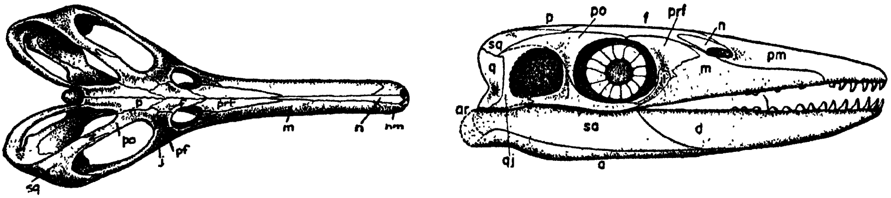


FIG. 165.—*Left*, dorsal view of skull of *Champsosaurus*, a late Cretaceous and early Tertiary amphibious form, length about 13½ inches. (After Brown.) *Right*, lateral view of the skull of *Thalattosaurus*, a problematical Triassic aquatic reptile; the skull is incomplete posteriorly; length about 1 foot. For abbreviations see Figure 96. (After Merriam.)

Most of the diagnostic characters of the rhynchocephalians are primitive ones to which little reference need be made. The palate is as primitive as that of *Youngina*, the pineal eye is still present, the vertebrae are amphicoelous rather than having the solid structure of most land reptiles of post-Triassic times. There have been some changes from primitive conditions, however: the lacrimal, supratemporal, and tabular bones have disappeared; the ribs attach to both arch and centrum by a single broad head rather than a double one; and (as in many other types) a large opening has developed in the primitively platelike ventral part of the pelvis.

Sphenodon appears to be a persistent survivor of an ancient group, for

Homoeosaurus (Fig. 167) of the Jurassic appears to have been almost identical in structure, and the ancestry of this type may without doubt go back through some imperfectly known Triassic genera to such a form as *Youngina*. Very few changes are needed to make a rhynchocephalian out of an eosuchian.

Early offshoots of the stock were the rhynchosaurs of the Triassic (Fig. 168). These tended to be of comparatively large size, but the postcranial skeleton and most of the skull were essentially similar to that of *Sphenodon*. The pineal opening had disappeared, however, and the beak was much elongated and toothless, with the nares fused into a single opening above it. *Rhynchosaurus*, *Hyperodapedon*, and related forms appear to have been shell-eating, shore-living types; they have been found in nearly all continents except North America.

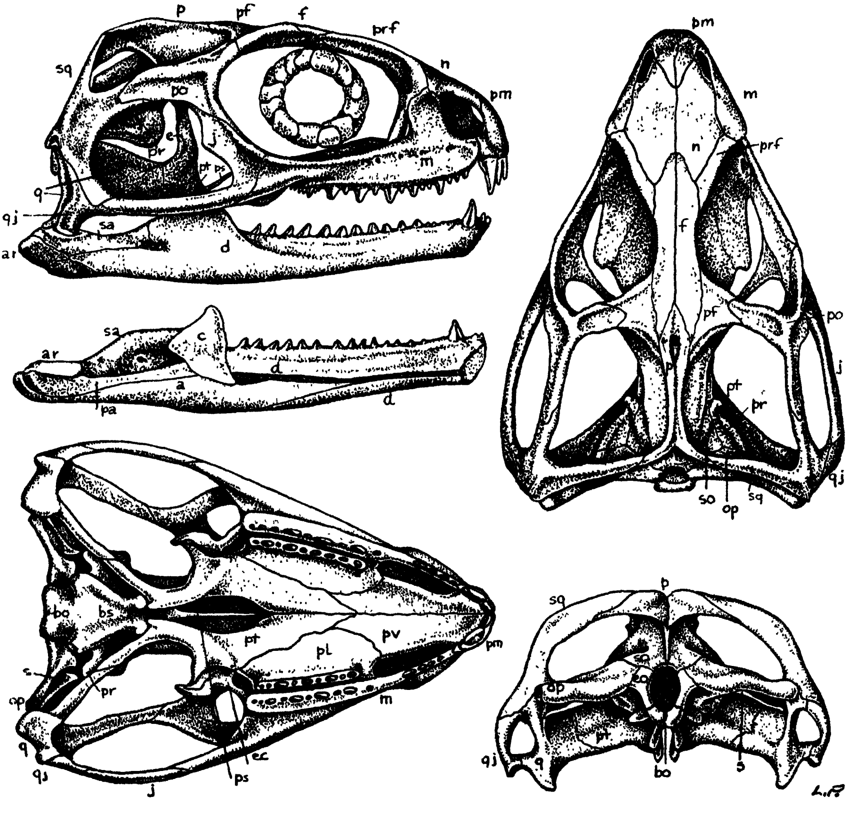


FIG. 166.—The skull of the living rhynchocephalian *Sphenodon*. *so*, Supraoccipital. For other abbreviations see Figure 96.

The Squamata.—The order Squamata includes the lizards and snakes, the most successful of modern reptiles. The lizards may be traced back to the Jurassic and had an interesting marine development in the Cretaceous. The snakes, last evolved of any reptilian group, appeared only in the Cretaceous and have obviously been derived from a lacertilian stock. A diagnostic feature of the lizards lies in the fact that there is but a single temporal opening—the upper one, lying above a bar formed by the postorbital and squamosal (Fig. 169). Instead of a lower opening's being present, we find that the cheek region lies open at the side behind the eye; the quadratojugal has disappeared; and the squamosal is much reduced. As a result of this loss of cheek covering, the quadrate bone is freely movable, giving greater flexibility to the jaws. The pineal eye persists in most lizards. The lacrimal bone is small or absent, the postparietal has gone, and so has either the tabular or the supratemporal (there is a single bone to represent the two). On the other hand, some lizards have developed a whole series of new superficial dermal bones which may cover the whole skull roof.

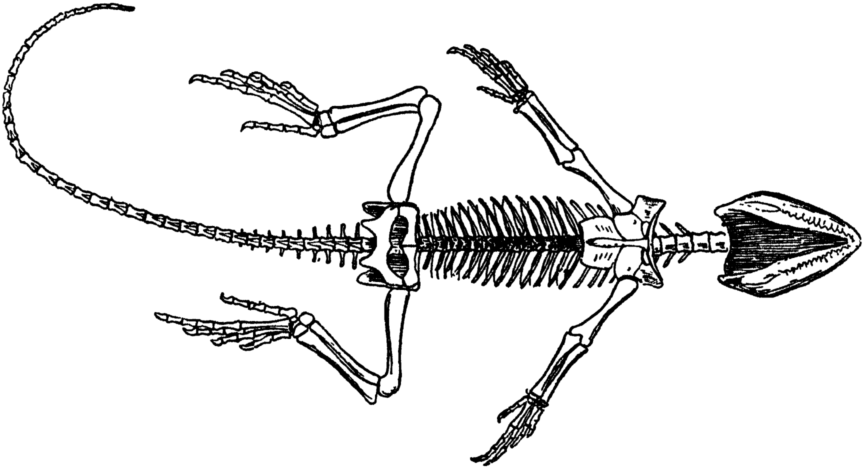


FIG. 167.—*Homoeosaurus*, a Jurassic rhynchocephalian in ventral view, about 7½ inches long. (From Williston's *The Osteology of the Reptiles*, by permission of the Harvard University Press.)

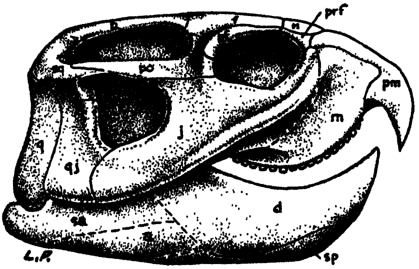


FIG. 168.—The skull of the Triassic rhynchosaur *Hyperodapedon*, length about 7½ inches. For abbreviations see Figure 96. (After von Huene.)

The palate is of the primitive type seen in many Permian reptiles and in

Sphenodon. The teeth are not set in sockets but are fused to the edge (as in *Sphenodon*) or, more commonly, to the inner sides of the jaws (pleurodont) and are thus specialized in character.

The primitive amphicoelous type of vertebra has persisted in a few living lizards, but in most of the Squamata a good articulation between the centra has been brought about through the development of the procoelous condition in which the swollen posterior end of one vertebra fits into a socket in the one behind (Fig. 146, *G*). The ribs have, as in *Sphenodon*, a single head; but, in contrast, this is narrow here and articulates only with the centrum. In other than these features the general structure is not unlike that just described for the Rhynchocephalia and may not be far from that of the eosuchians.

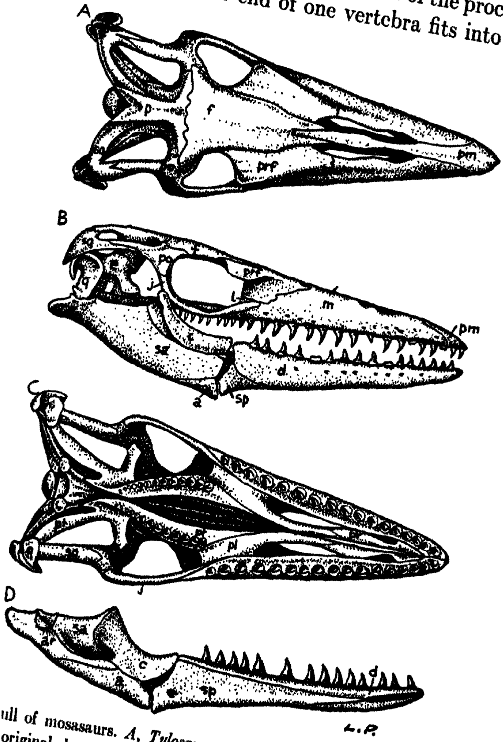


FIG. 169.—The skull of mosasaurs. *A*, *Tylosaurus*, dorsal view, original about 38 inches long; *B*, *Clidastes*, lateral view, original about 20 inches long; *C*, *Platecarpus*, ventral view, original about 22 inches long; *D*, inner view of jaw of *Clidastes*. For abbreviations see Figure 96. (After Williston.)

Origins.—With regard to the origin of lizards there have been two sharply contrasted views. There is but a single temporal opening. This was held by some to be a primitive character, the lizards supposedly having come from some protorosaur such as *Araeoscelis*. But the temporal region of that little reptile shows none of the excavation at the side which characterizes the lizards, and there are few positive resemblances. On the other hand, *Sphenodon* and some lizards are exceedingly similar in nearly every anatomical feature except the temporal region. We may thus reasonably assume that the lizards, like the rhynchocephalians, have come from the primitive Eosuchia. The lizard temporal region may be interpreted as derived from a diapsid condition by loss of the lower temporal bar; and we have seen that *Prolacerta* shows almost diagrammatically an intermediate stage in this process.

Lizards.—The Squamata are divided into two suborders: the Lacertilia, the lizards; and Serpentes (or Ophidia), the snakes. The first are, of course, the more primitive of the two and the first to be represented in the fossil record. Even the lacertilians, however, were comparatively late in appearance; for there are no certain fossil lizards in rocks older than the Jurassic and it was only at the end of the Mesozoic and in Tertiary times that the group became a flourishing one.

There are a large number of families of lizards, few of which need be mentioned in detail. There are various methods of classifying them; we shall employ a system in which the lizards are considered as constituting some seven infraorders:

Gekkota.—The geckoes, mainly from the Old World, have amphicoelous vertebrae which suggest that the group is a primitive one; unfortunately, no fossil forms have been identified.

Iguania.—The iguanids are common, and often large, New World lizards; the agamids, Old World relatives. The group includes lizards of rather primitive character, and both families have been identified in the Upper Cretaceous.

Rhiptoglossa.—The chameleons, highly specialized African forms, not certainly identified in the fossil state.

Scincomorpha.—A large and varied group of lizards, named from the skinks but including also certain burrowing and limbless lizards, the European lizard *Lacerta*, etc. Several families of this group are known from the Eocene onward, and it is possible that *Ardeosaurus* of the Upper Jurassic, one of the earliest of lizards, is related to the skink group.

Amphisbaenia.—Very wormlike subterranean lizards. In the small skull the bones are arranged in compact fashion in correlation with burrowing habits, giving a structure comparable to that of the Apoda among the Amphibia. Probably of scincoid derivation, the amphisbaenians appear in the Eocene.

Anguimorpha.—Advanced forms, including the Gila monster (*Heloderma*), the slow worms (*Anguis*), and a variety of genera many of which are limbless. Bony scales or osteoderms, although present in some other lizards, are most highly developed in this group. Members of the Anguidae appear in the Cretaceous, and the group may be represented even in the Jurassic.

Platynota.—The living members of this group, the monitor lizards of the Old World, form the family Varanidae. An East Indian monitor attains the length of a dozen feet; and *Megalania*, a Pleistocene fossil, was perhaps double that size. The marine lizards discussed below are also members of the Platynota; and, although the varanids have stout limbs, many features indicate that they are closely related to the ancestry of the snakes. Key characters include the development of a flexible joint in the middle of each lower jaw and the complete inclosure of the front part of the brain cavity in bone. Varanids appear in the Upper Cretaceous, but it is obvious from a phylogenetic standpoint that the ancestral platynotans must have developed before the end of the Jurassic.

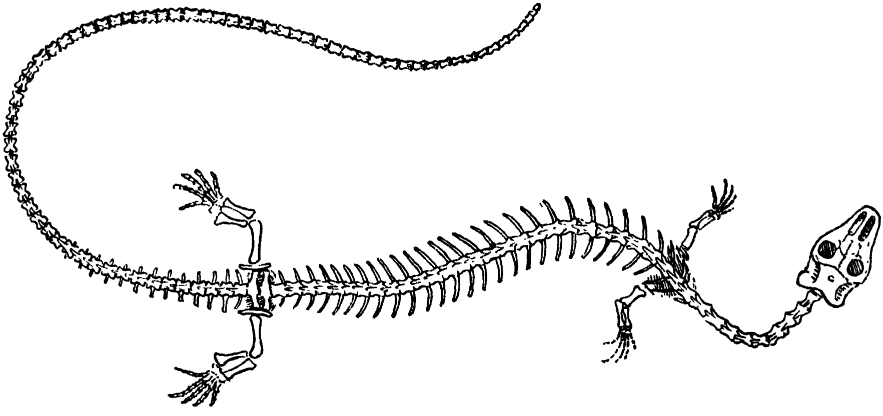


FIG. 170.—*Adriosaurus*, a Lower Cretaceous semiaquatic lizard; original about 16 inches long. (From Williston's *The Osteology of the Reptiles*, by permission of the Harvard University Press.)

Marine lizards.—The one striking series of fossil lizards is that of the varied marine forms of the Cretaceous, which are quite surely members of the Platynota and closely related to the monitors.

Two groups of aquatic lizards appear in the Lower Cretaceous. The dolichosaurs, including *Adriosaurus* (Fig. 170) and the somewhat later *Dolichosaurus*, were small forms with a very long neck and limbs of a fairly normal structure; these lizards were not completely adapted for marine life. Their great body elongation indicates that they were not the ancestors of the other water-living lizards. The aigialosaurs were a second early Cretaceous group, also fairly small and also only semiaquatic in their probable habits. Here the neck was short, and there was a powerful swimming tail.

From the last, apparently, came the mosasaurs (Figs. 169, 171), Upper Cretaceous marine lizards, world-wide in distribution but especially common in the chalk rocks of Kansas; *Platecarpus* and *Tylosaurus* are among the best-known types. They were of large size, averaging about 15–20 feet in length. There was a long head, a short neck, and a long slim body and tail. The tail was the main swimming organ, the limbs functioning as steering organs. In the paddles (Fig. 147, *E*), as usual in aquatic forms, the proximal bones were much shortened; but the toes were well developed, spreading, and presumably webbed. The normal number of digits was present, but there was a slight increase in the number of joints. The skull was much like that of the varanid lizards; and, as in them, there was a well-developed joint midway of the jaws, between angular and splenial. The teeth were rather unlike those of most lizards in that they were set in pits rather than fused to the jaws.

The mosasaurs were mainly fish-eaters, probably existing on the large variety of primitive teleosts which were their contemporaries. There were various types, presumably diving, deep-sea, and surface forms. A more divergent form was *Globidens*, which is poorly known except for the jaws. The teeth had peculiar spheroidal crowns, and it would seem that this form was a mollusk-eater.

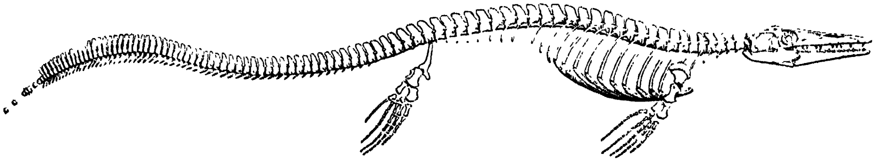


FIG. 171.—*Tylosaurus dispar*, a mosasaur from the Niobrara Chalk of Kansas; original about 26 feet long. (From Osborn.)

Despite the profusion of mosasaur types in the late Cretaceous rocks, they perished as soon as did their contemporary fellow-fishermen, the plesiosaurs.

Snakes.—The Serpentes, snakes, are the newest of reptilian groups. Obviously derived from varanid types, they first appeared in the Cretaceous but are not well known as fossils.

In snakes almost all traces of limbs are lost, as in some of the true lizards. The limbless condition seems to be associated with the fact that in all slimly built reptiles locomotion, even with limbs, utilized to some extent the sinuous motion of the body held over from the fish stage; the legs merely held the ground gained by twisting the body. With the development of a freely movable rib system to aid in sinuous movement and the addition of horny scales, which could hold onto the surface and prevent a backslip, the loss of legs became a possibility, and a new type of locomotion made its appearance.

In snakes the vertebrae may increase in number up to several hundred, with, of course, little regional differentiation, and extra articulations are present between the vertebrae (Fig. 146, *G–I*). The skull (Fig. 172) has been highly modified in the direction of greater motility of its components for swallowing of large prey. Even the upper arch of the cheek is lost, leaving the quadrate very loosely attached to the skull. The quadrate also has but a loose connection with the palate, while the palate and the anterior portion of the skull may both move freely on the braincase region. The dentary is freed considerably from the more posterior elements of the jaws, and the two branches of the jaw are connected only by ligaments. These all make for the possibility of a wide jaw gape. The teeth are usually directed backward, so that alternate jaw movements tend to push the prey down the throat. The pineal opening is lost. The parietal and frontal have grown down so that, together with a new ossification, they completely inclose the front of the braincase, a rather necessary feature for brain protection during the swallowing of large objects.

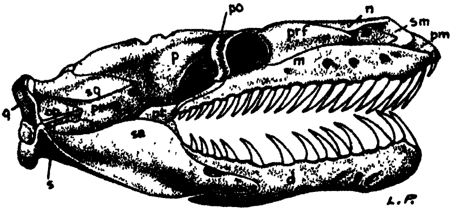


FIG. 172.—Skull of a primitive living snake, the python. For abbreviations see Figure 96. (After Williston.)

The oldest-known snakes of the late Cretaceous and Eocene, such as *Palaeophis*, appear to have been rather primitive forms with fairly short bodies and stout build, many of them of large size; the boas and pythons seem to be little-modified descendants. The harmless smaller snakes, such as the grass snakes and many other types included in the family Colubridae, do not appear until the Oligocene. Poisonous snakes with grooved or hollow fangs seem to have been a late development, not surely known before the Miocene. Some such types, with poison-bearing teeth in the back of the jaws, are included among the existing Old World members of the colubrids but are unknown as fossils. More progressive forms, with anteriorly placed fangs, are the cobras (Elapidae), with fixed fangs, and the vipers (Viperidae) and pit vipers, such as the rattlesnakes (Crotalidae). In the last two families the palatal bones are so arranged that the fangs are automatically turned down and in when the mouth closes and are erected when it opens.

CHAPTER 11

RULING REPTILES

THE mutual relations of many of the reptilian types are, as has been seen, none too clear, and the establishment of superordinal or subclass groups is a dubious matter. In contrast are the groups now to be considered—a series of orders including the crocodiles, dinosaurs, flying reptiles, and related primitive forms which may be unified in the subclass Archosauria, the ruling reptiles (Fig. 173).

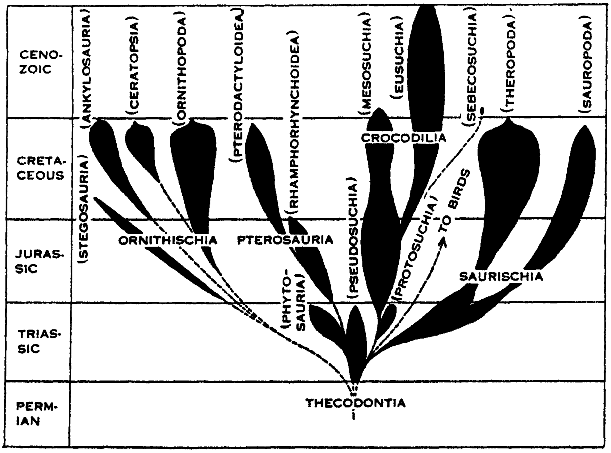


FIG. 173.—The phylogeny of the archosaurian reptiles

Diagnostic characters possessed by all these forms are few. All possess two temporal openings—the diapsid condition; but two openings are also present in rhynchocephalians and other reptiles which seemingly have little to do with the groups under consideration. Of greater importance are the comparable evolutionary trends seen in the development of the various orders and indicative of the potentialities inherent in the ancestral stock. Many similarities in structural features among end-forms of different archosaurian lines have not been inherited as such from a common ancestor but have been independently acquired. This, however, does not debar such characters from consideration as indications of relationship. Study of fossil forms increasingly indicates that there has been an enormous amount of parallelism in development; but this study also appears to demonstrate that close parallelism occurs only in closely related forms.

Bipedalism.—The most characteristic archosaurian evolutionary tendencies are to be seen in the limb-and-girdle structure and are connected with significant changes in the locomotion of most members of the group.

The clumsy style of walking of the primitive cotylosaurs was improved upon by later reptiles in various ways. Many reptilian orders tended merely to improve a four-footed style of progression; the archosaurs are unique in that they tended toward a bipedal gait, the animal running semi-erect on its hind legs. Some of the most primitive archosaurs had hardly begun the changes leading to bipedalism, and some groups never attained this condition. Others, having once acquired a bipedal gait, have slumped back to a four-footed pose; but even in such forms the group history has left structural marks.

In the archosaurian bipedal pose the anterior part of the body tilts forward at a considerable angle from the pelvis. This posture could not be maintained without a tail as a balancing organ, and this structure is almost always long and powerful. In addition to its balancing function, it also sheathes powerful muscles which move the hind limbs.

This changed position has entailed many structural changes in the limb bones. The entire weight of the body in bipeds is supported from the hips; and the sacrum is strongly built, a number of ribs in addition to the primitive two usually being incorporated in it. The ilium is elongated, and the acetabulum lies high up near the backbone. The body could not, of course, be supported in a biped with the legs spread out at the side of the body. Instead, the hind legs have been turned forward, giving them a fore-and-aft motion, and are considerably straightened, so that essentially they form two long and powerful pillars extending from the pelvis to the ground.

The head of the femur now lies under the upper margin of the socket of the acetabulum and no longer pushes in against it, and the bottom of the cavity usually becomes open. The femur (Fig. 174), originally straight, develops a head at the side of its upper end to fit into the acetabulum, while, part way down, an extra process—a fourth trochanter—is often developed for the attachment of tail muscles. The tibia tends to become long, the fibula reduced in importance. An extra joint, making for additional speed, may be added to the leg by an elongation of the metatarsal elements. The tarsal bones, which might become an element of weakness in this new type of limb, tend to be reduced, the proximal ones sometimes fusing with the tibia and fibula, the distal ones becoming associated with the heads of the metatarsals; this leaves but a single movable joint in the middle of the tarsus. With the forward turning of the limb, the foot, originally twisted, extends straight forward from it; and the central, rather than the lateral, toes tend to be the more highly developed. The third toe often becomes the longest of the set; the second and fourth, at either side, slightly shorter. The remaining toes usually become comparatively unimportant, the fifth often disappears entirely, while the first is sometimes turned backward, apparently acting as a prop. Although the comparative length of the toes may be greatly changed, the number of joints has tended to remain constant; and in forms as far apart as carnivorous dinosaurs and birds the feet are almost identical in structure and in phalangeal formula.

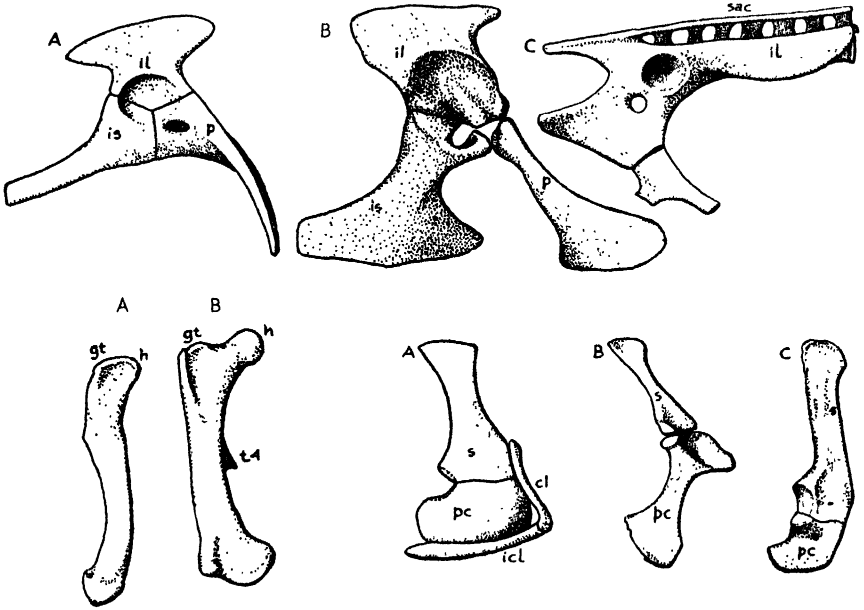


FIG. 174.—Girdle and limb elements of archosaurs. *Above*, pelvic girdles: *A*, The thecodont *Aetosaurus; B*, the Jurassic crocodile *Steneosaurus; C*, the Cretaceous pterosaur *Pteranodon*. Abbreviations: *il*, ilium; *is*, ischium; *p*, pubis; *sac*, sacrum. In *C* the homologies of the ventral element are uncertain. (*A* after Broom; *B* after Andrews; *C* after Eaton.) *Lower left*, anterior views of right femur of *A*, a crocodilian; *B*, a trachodont dinosaur. Abbreviations: *gt*, greater trochanter for attachment of iliac muscles; *h*, head, fitting into acetabulum; *t4*, fourth trochanter for attachment of caudal muscles; *Lower right*, shoulder girdles of archosaurians: *A*, the thecodont *Euparkeria; B*, the Jurassic crocodile *Steneosaurus; C*, the sauropod dinosaur *Morosaurus*. Abbreviations: *cl*, clavicle; *icl*, interclavicle; *pc*, precoracoid; *s*, scapula. (*A* after Broom; *B* after Andrews; *C* after Marsh.)

A characteristic series of modifications takes place in the pubis and ischium (Fig. 174, *top row*). Instead of retaining the primitive platelike structure, both bones tend to be elongated and directed downward, thus producing, with the ilium, a triradiate type of pelvis. This structural feature is probably related to the fact that, with the femur playing back and forth close to the body, the muscles running to it from these bones must shift fore or aft to gain a longer play. Even the most primitive of archosaurians show at least the beginning of this tendency, while some forms have a still more complicated pelvic structure.

The front legs have naturally become less important with the development of the bipedal gait. They are usually considerably shorter and much weaker than the hind legs. There is some tendency toward a loss of fingers in the more advanced forms, and but two or three of the inner ones may persist. Certain dinosaurs which have become quadrupedal again seem to have effected some secondary redevelopment of the front legs, but even in most of these the anterior limbs are much shorter than the hind ones. In the shoulder (Fig. 174, *lower right*) there is only a single coracoid bone, and the scapula tends to be rather long and slim. The cleithrum is lost, as in most advanced reptiles; and clavicles or interclavicle or both may drop out.

Skull.—The primitive archosaurs were carnivores with simple, pointed teeth set in separate sockets on the margins of the jaws; in contrast with most other reptiles, teeth have disappeared from the palatal bones in all except a few primitive forms. In some cases there is a tendency for some or all of the teeth to be lost and to be replaced by a horny bill, and the cheek teeth were sometimes modified for plant feeding. A pineal opening is almost invariably absent. With the effect of lightening the skull, an antorbital fenestra is usually present between the orbit and the nostril. The quadrates are large and extend far up the back corners of the skull. The two pterygoids have tended to meet to form a median plate in the roof of the mouth, with palatal vacuities present at either side. In the lower jaw appears a fenestra between dentary, angular, and surangular.

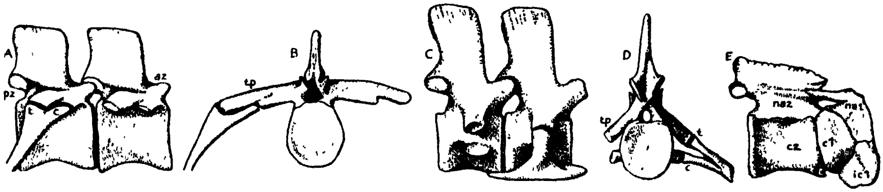


FIG. 175.—Vertebrae of the Jurassic crocodile *Steneosaurus*. *A*, Dorsal vertebrae; *B*, same, anterior aspect; *C*, cervicals; *D*, same, posterior aspect; *E*, atlas and axis. Abbreviations: *az*, anterior zygapophysis; *c*, capitulum of rib; *c1*, *c2*, centra of first and second vertebrae (atlas and axis); *icl*, intercentrum of atlas; *na1*, *na2*, neural arches of atlas and axis; *t*, tubercle of rib; *tp*, transverse process of neural arch. (After Andrews.)

The ribs almost always retain the primitive double-headed condition. But a common archosaurian feature is the tendency for the two heads to crowd closer together; in the cervical region the capitulum moves back to arise from the centrum below the transverse process, and in the trunk both heads may arise from the process itself (Fig. 175).

Thecodonts.—The characters and tendencies just discussed are seen in the various advanced archosaur types—the dinosaurs, pterosaurs, and crocodiles—and in the primitive birds (which seem clearly derivable from the archosaurs). These forms make their appearance in the late Triassic and Jurassic. We should expect to find in the strata deposited during the first-mentioned period the ancestors of the later ruling reptiles, a common stock in which archosaurian characters were first making their appearance.

Such a group is that which we shall here consider as comprising the order Thecodontia. In it are included a number of types of Triassic reptiles which vary considerably among themselves but which, as a whole, show the initiation of archosaurian tendencies.

The two-arched condition of the skull had already been acquired by some reptiles in late Permian times. The early diapsids which we have treated as constituting the Eosuchia are possibly ancestral to the primitive ruling reptiles but show almost no suggestion of true archosaurian characters.

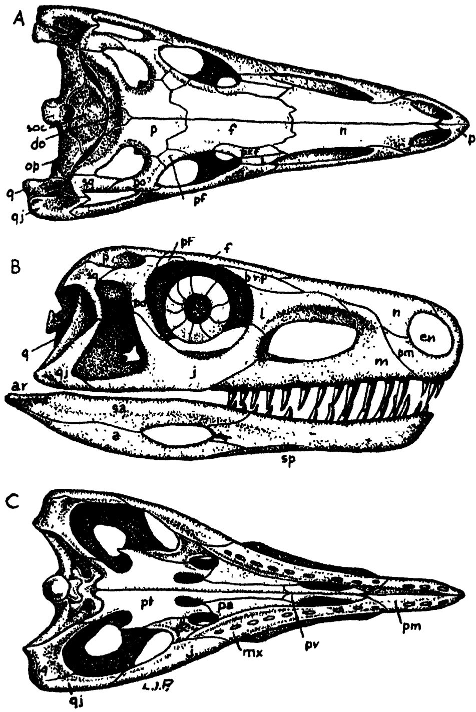


FIG. 176.—The skull in thecodonts. *A*, Dorsal, and *B*, lateral views of *Euparkeria*, skull length about 6 inches; *C*, palate of *Ornithosuchus; pa*, palatine. For other abbreviations see Figure 96. (*A*, *B* after Broom; *C* after Newton and von Huene.)

Primitive thecodonts.—Quite in contrast are a number of Triassic forms, such as *Euparkeria* (Fig. 176, *A*, *B*), *Ornithosuchus* (Fig. 176, *C*), and *Saltoposuchus* (Fig. 178), forming the suborder Pseudosuchia. Such types are well known from both Europe and South Africa and were probably world-wide in distribution. They were, in the main, small reptiles with about the range of size seen in modern lizards, and the general appearance, as well, may have been rather lizard-like. Here, however, the comparison ends, for not only the bipedal gait which seems to have been developing but many internal features emphasize their position as ancestors of the later ruling reptile orders.

These forms were active little carnivores, with sharp teeth set in sockets in the thecodont fashion characteristic of the subclass. The skull was long and slim, with the nostrils near the front end. In contrast with the two-arched reptiles considered in the last chapter, an antorbital vacuity was developed, the upper temporal opening was comparatively small, the pineal eye had disappeared, and the tabulars and postparietals were gone; on the under side of the skull, palatal teeth had vanished, palatal vacuities were present, and the two pterygoids were in close contact, In all these skull characters the members of this group were typical archosaurs.

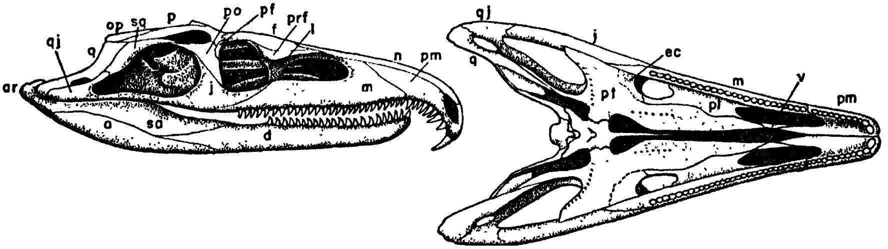


FIG. 177.—Lateral and ventral views of the skull of *Chasmatosaurus*, a Lower Triassic thecodont with primitive palatal structure; length about 18 inches. For abbreviations see Figure 96. (After Broili and Schroeder.)

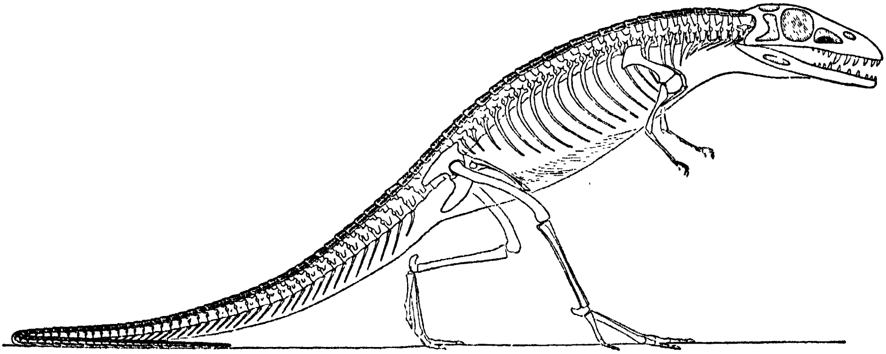


FIG. 178.—*Saltoposuchus*, a lightly built Triassic thecodont, about 3¾ feet in length. (From von Huene.)

In their postcranial skeletons they exhibited the beginnings of archosaurian bipedal tendencies. The hind legs were very much longer than the front ones. The pelvis (Fig. 174, *A*, *upper row*), while always somewhat platelike, showed some elongation and down-turning of both pubis and ischium; the metatarsals were somewhat elongated, the third toe tended to be longer than the others, and the fifth toe seems to have been considerably reduced. On almost all of them there were protecting rows of small bony plates down the back.

Types such as these were apparently numerous in early Triassic times and persisted to the end of the period. It is obvious that they occupy a central position in archosaruian evolution. Almost no structural features need to be changed to turn some forms into primitive carnivorous dinosaurs, and other related genera seem to show the beginning of the secondary palate which characterizes the crocodiles. Known forms are somewhat farther in structure from the other archosaurian types, but there is nothing in their structure to debar them from a position of ancestry to pterosaurs or the "birdlike" dinosaurs.

There are numerous variations among the thecodonts from the typical pattern described above. *Chasmatosaurus* (Fig. 177), for example, is a form from the Lower Triassic of South Africa which was somewhat specialized in the presence of an overhanging beak rather analogous to that of rhynchosaurs, but very primitive in its palatal construction. Palatal teeth were still present, and the movable articulation of palate with braincase, lost in all typical archosaurs, still persisted. *Erythrosuchus* was a large South African Lower Triassic form in which bulkiness was the structural keynote. The body was stout, the tail short, the limbs comparatively heavy, and the hind legs but little longer than the front. The skull was comparatively short, although rather high. It has been suggested that the creature was a marsh dweller. Its sharply pointed teeth lead us to assume that it was a carnivore, but with its clumsy build it is difficult to imagine its source of food supply. *Aetosaurus* of the European Upper Triassic was a small thecodont much like those described above except that it had developed a complete incasing armor of bony plates. Also heavily armored, but very different in other respects, was *Episcoposaurus* [*Desmatosuchus*] (Fig. 180) of the American Triassic. In this large animal, comparable in bulk with the contemporary phytosaurs, broad plates had completely covered the back, and the limbs were protected by hornlike bony processes which curved down over them

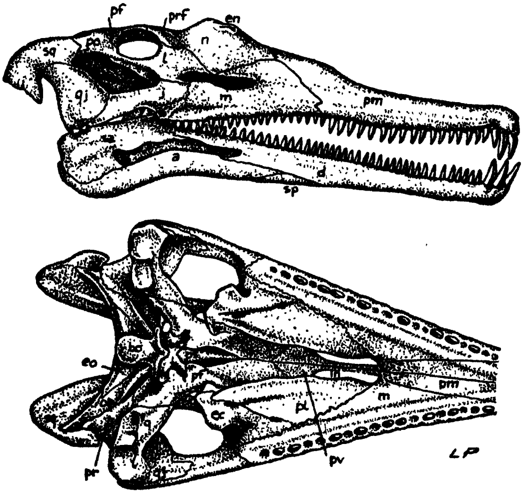


FIG. 179.—Lateral view of skull and posterior part of palate of the phytosaur *Machaeroprosopus;* skull length about 3½ feet. For abbreviations see Figure 96. (After Camp.)

and must have hindered an attack by carnivores. The skull was short and, while difficult of interpretation, not at all like that of phytosaurs.

Phytosaurs.—Among the most abundant of fossil reptiles from the later Triassic are the phytosaurs. These specialized thecodonts appear to have been quite similar in habits and general appearance to the modern crocodiles and were ecologically the predecessors of these forms, although not in themselves directly ancestral. The skull (Fig. 179) was much elongated in correlation with probable fish-eating habits, and the jaws were armed with a powerful battery of sharp teeth. The position of the nostrils was one seen in other water-living types, the external openings being far back, almost between the eyes. The two openings were close together near the top of the skull and were in some cases situated in a sort of crater rising above the level of the skull top; this seems to have been a device for breathing with most of the body under water.

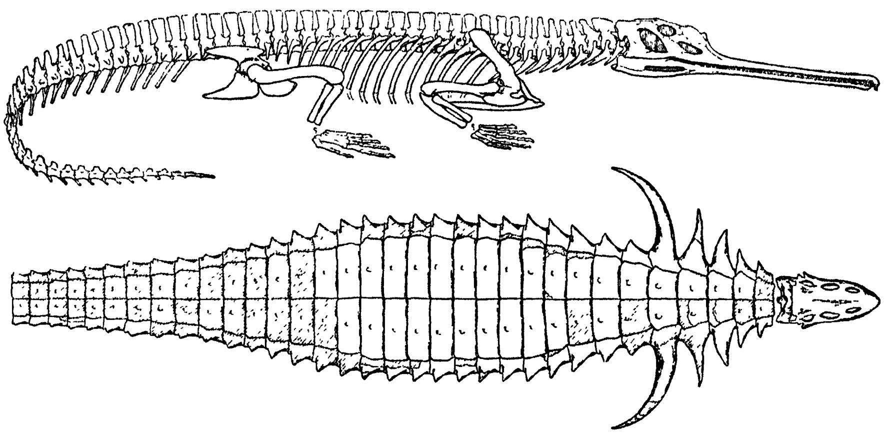


FIG. 180.—*Above, Mystriosuchus*, a Triassic phytosaur. Original about 11½ feet long. (From McGregor.) *Below, Episcoposaurus* [*Desmatosuchus*], an armored thecodont from the Triassic of North America, dorsal view. Part of body illustrated about 12 feet in length. (From Case.)

The body (Fig. 180) was crocodilian in general shape. The limbs were short, and the pelvis primitive in structure. But the hind legs were considerably longer than the front ones, although, with the taking-up of an aquatic life, these animals had completely given up any aspirations toward bipedalism.

A considerable variety of these forms—*Phytosaurus, Mystriosuchus, Machaeroprosopus*, and many other genera—were present in Europe and North America, although apparently absent from the Southern Hemisphere. Almost all are from the Upper Triassic; a single poorly known form from the Lower Triassic of Europe appears to be relatively primitive and may be leading back toward the more generalized thecodont type. The phytosaurs were comparatively successful for the time but apparently failed in competition with the crocodiles and disappeared at the close of the Triassic.

The history of the thecocodonts was a brief one. But their development was an event of the greatest importance in the evolution of Mesozoic life, a necessary prelude to the later expansion of ruling reptile types.

Of the forms descended from this group, the dinosaurs and birds will be treated in later chapters; we shall include here an account of the other archosaurian orders—the crocodiles and flying reptiles.

Crocodiles.—The crocodiles and alligators and their relatives, the order Crocodilia, have been among the least progressive of ruling reptiles but nevertheless are the only members of the archosaurian stock which survived beyond the Age of Reptiles. Derived from the thecodonts in the late Triassic, they have undergone comparatively little modification in later times. In general body form and in many structural features they are not far from the primitive archosaurian type, and in their amphibious mode of life they resemble greatly their somewhat distantly related predecessors, the phytosaurs.

The skull (Fig. 181) in many respects is of a primitive archosaur pattern; it is always rather elongate and extremely so in fish-eating types, such as the living Indian gavial. The palate, however, is much modified. We have seen that in the phytosaurs breathing difficulties were overcome to a considerable extent by shifting the external opening of the nostril far back, the internal opening beneath consequently lying in the back part of the mouth. In the crocodiles the external nares are at the tip of the snout, so that breathing can be accomplished even if only this part of the body is exposed, while internally the danger of shipping water into the air supply is prevented by the development of a secondary palate. Below the original inner opening of the nostrils the premaxillae, maxillae, and palatines have formed a secondary shelf which extends backward parallel to the primary roof of the mouth; the air passes back above this new palatal structure to the posteriorly situated internal nares. In modern forms even the pterygoids have met in the midline and formed a further prolongation. As a result, the inhaled air does not enter the mouth proper at all but passes back separately into the throat, which can be closed off by a flap of skin. A similar secondary palate has been formed in mammals but almost never developed to the extent seen in the crocodiles.

The general body shape is rather lizard-like, with a long flattened tail which is the main swimming organ. In modern forms the vertebrae are not hollowed or flat-ended structures but are procoelous. There is always a well-developed set of dermal armor plates down the back beneath the horny scales, and sometimes down the ventral side as well—a feature which is an inheritance from the primitive thecodonts.

The modern crocodiles are quadrupeds and, as ordinarily observed, have a slow, sprawling gait. Fast locomotion, however, is accomplished with the body high off the ground and the limbs straight under the body, as in all advanced archosaurians; and, while crocodiles are not bipeds, it is suggestive that the front legs are always much shorter than the hind. The contrast in length was very strongly marked in the earliest Jurassic types, and it is highly probable that some degree of bipedal locomotion had developed in the archosaurian ancestors of the group before a trend toward an aquatic life appeared. In the shoulder (Fig. 174) an interclavicle is retained, but the clavicles are lost. The two outer fingers of the front foot are reduced in a common archosaurian fashion, while, as in dinosaurs, the carpals are much reduced,

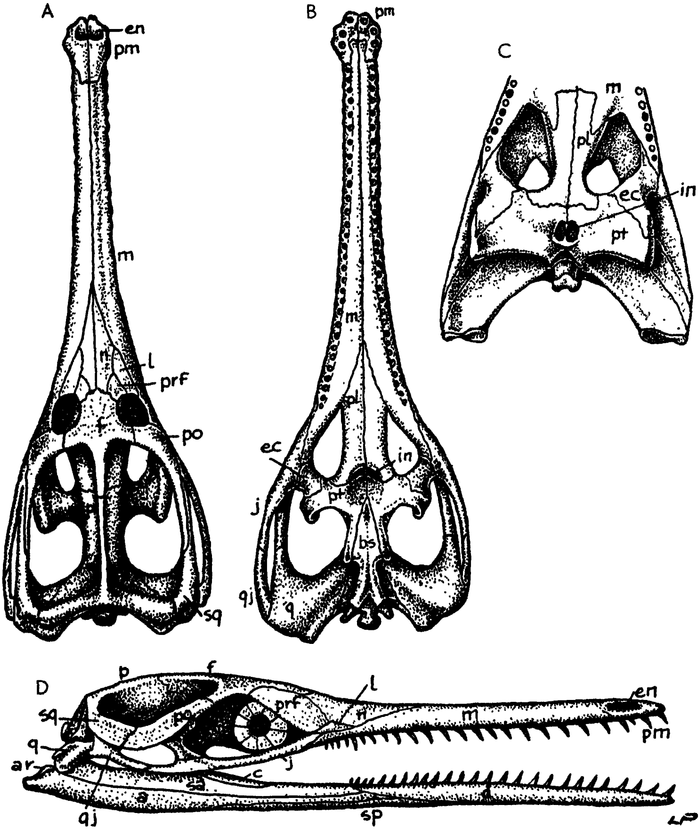


FIG. 181.—The skull in crocodilians. *A*, Dorsal, and *B*, ventral, views of the Jurassic *Steneosaurus*, skull length about 30 inches; *C*, part of palate of the Eocene *Crocodilus affinis*, to show posterior movement of internal nares; *D*, lateral view of the Jurassic marine crocodile *Geosaurus*, skull length about 15 inches. For abbreviations see Figure 96. (*A*, *B* after Andrews; *C* after Mook; *D* after Fraas.)

leaving only two proximal and one distal element; the proximals are usually much elongated (Fig. 182, *A*). There are but two sacral ribs, a primitive feature. The pelvis (Fig. 174) has a triradiate structure, with pubis and ischium extending down separately from the acetabular region, much as in the saurischian dinosaurs. The crocodile pelvis is peculiar, however, in that the pubis has been excluded from the acetabulum by the ischium. The hind legs are quite long; as in most archosaurians, there is some elongation of the metatarsals, and the fifth digit is reduced to a stump of the metatarsal. But the foot (Fig. 182, *B*) is somewhat divergent from that of many other archosaurs in that the first toe is still in line with the others, the fourth toe is slightly reduced, and the tarsus has a joint at its proximal end rather than in the middle.

The Crocodilia may be grouped into four suborders: Protosuchia, very primitive Triassic forms; Mesosuchia, the typical Jurassic and Cretaceous families; Eusuchia, more progressive families, particularly of the Cenozoic; Sebecosuchia, established for a peculiar South American fossil type.

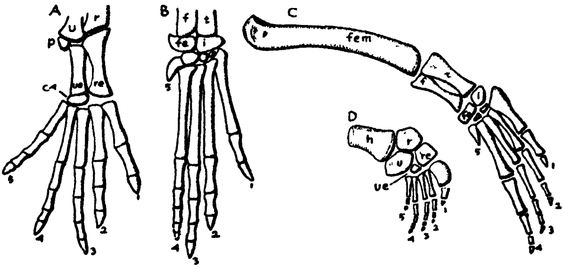


FIG. 182.—Limbs of crocodilians. *A*, Manus, and *B*, pes, of the Jurassic *Alligatorellus; C, D*, hind and front legs of the Jurassic marine crocodile *Geosaurus*. The digits are numbered. Abbreviations: *c4*, fourth distal carpal; *f*, fibula; *fe*, fibulare; *fem*, femur; *h*, humerus; *i*, intermedium; *p*, pisiform; *r*, radius; *re* radiale; *t*, tibia; *u*, ulna; *ue*, ulnare. (*A, B* after Lortet, *C, D* after Fraas.)

Ancestral crocodiles.—Except for palatal structure and such details as the exclusion of the pubis from the acetabulum, crocodile anatomy is not remote from that of their thecodont ancestors; and, unless these features were preserved in a specimen, it would be difficult to tell an ancestral crocodile from a member of the Thecodontia. Several thecodont-like reptiles of the later Triassic are thought to be transitional to the crocodiles; and in one case —*Protosuchus* of the Upper Triassic of North America—it seems sure that we are dealing with a form in this category. The palate is incompletely preserved in the single known specimen, but the pelvis shows clearly the typical crocodilian specialization. In other respects *Protosuchus* resembled the small armored thecodont types from which it undoubtedly had been derived.

Mesosuchians.—In the Jurassic there appears an abundance of crocodiles, no longer transitional in nature but definitely members of the order.

These forms, and most of those of the Cretaceous as well, show, however, a few features in which they are definitely more primitive than surviving types. The upper temporal openings were not so small as in living forms; the internal nostrils still lay between the palatine bones, for the pterygoids had not yet been pressed into service to continue the secondary palate; the vertebrae still retained flattened or even slightly hollowed ends; and the antorbital opening found in many other archosaurs had not disappeared in some cases (it is absent in all later crocodiles). These older fossils may be conveniently placed in a suborder Mesosuchia.

The Jurassic is dominantly marine in its sediments, and hence our knowledge of crocodiles of this period is mainly confined to side lines of the group; these tend to be long-snouted forms which may, in general, have been fish-eaters. *Teleosaurus* and *Steneosaurus* (Fig. 181) are representative of a family of such crocodiles; these include the oldest-known mesosuchians, for they are present in the Liassic deposits of the Lower Jurassic; other crocodiles do not appear until later in the period. *Pholidosaurus* is representative of another long-snouted Upper Jurassic group which appears to have lived in fresh waters or estuaries and which may have given rise to *Dyrosaurus* and other genera which persisted into the early Tertiary.

The teleosaurs were apparently marine but retained much of the normal body build of the group; from them not improbably are descended a highly specialized marine group which flourished in the later Jurassic. *Metriorhynchus* and *Geosaurus* (Figs. 181, 182) are here considered as mesosuchians, but they are so distinctive in marine adaptations that many writers have classed them as a separate suborder, the thalattosuchians—sea crocodiles. They were unarmored crocodiles in which the limbs were considerably modified to serve as paddles, The main swimming organ was the tail, which had redeveloped into a fishlike tail fin rather similar to that of early ichthyosaurs, with the backbone turned down into the lower lobe of the fin, the upper lobe presumably being supported by toughened skin. These aquatic crocodiles were not uncommon in the late Jurassic seas, but for some reason they do not seem to have been so successful as were other reptilian marine types and soon disappeared.

Still further types were present in the late Jurassic. *Alligatorellus* and *Atoposaurus* were tiny crocodiles—one less than a foot in length—with reduced armor and with a very short broad skull. In most crocodilians the external nares are united into a single tubular opening; here they are still separated by a bar of bone in primitive fashion. *Notosuchus* and *Libycosuchus* of the Upper Cretaceous of South America and Africa are rather larger forms, but armorless and with similarly built short skulls, and are possibly descended from the atoposaurs.

All the families so far mentioned are side branches of the crocodilian stock;

the "main line" leading to later families appears to lie through *Goniopholis* and its allies of the late Jurassic and Cretaceous. The body build was normal in its construction; the skull was broad and moderately long, and the secondary palate extended farther back than in the more primitive mesosuchians.

Eusuchians.—In the typical Cenozoic crocodiles we find progressive features not present in the mesosuchians. A diagnostic feature (Fig. 181, *C*) is the extension of the secondary palate far back beneath the skull, so that the pterygoids, as well as the palatines, enter extensively into its construction. The vertebrae, earlier flat-ended, are procoelous in structure. The dorsal armor is retained, but that of the belly is absent except in some of the alligators. With a few Eocene exceptions, all post-Cretaceous crocodilians belong to the Eusuchia. Their origins, however, lay in the Mesozoic, for *Hylaeochampsa* of the European Lower Cretaceous was already a small eusuchian, presumably derived from the goniopholids.

Apart from some early specialized genera of the late Cretaceous, all the eusuchians may be ranged in three groups, usually considered as families—Crocodylidae, Alligatoridae, and Gavialidae. The distinction between the three is, however, none too sharp, and family assignments are often none too certain. The gavials, with a living representative in the Ganges, have a long slender snout, sharply marked off posteriorly from the rest of the skull. In the crocodile group the snout may be elongate but is broad as well; it is short in the alligators. A key character is the fact that in alligators the first mandibular tooth (and often the fourth as well) bites into a deep pit in the palate; in the crocodiles these pits are absent, but the upper jaw may be notched for the fourth lower tooth.

All three families were present in the Eocene in northern continental areas, and both crocodile and alligator types were abundant and varied in these regions in the early Tertiary; finds from the southern continents, too, are not uncommon. The wide early Tertiary distribution of the Crocodilia is but one of many lines of evidence suggesting that northern climates were at that time much more equable than today.

Sebecus.—A peculiarly aberrant form is *Sebecus*, of the Eocene of South America, which fits into neither mesosuchian nor eusuchian suborders. The snout, instead of being depressed, is high and narrow, giving the skull much the appearance of some of the phytosaurs. There is a secondary palate, but it is short and broadly open behind, so that there is no development of the typical crocodile tube for the air passages; and the teeth are compressed structures like those of predaceous dinosaurs. Relatives are unknown, but this genus must have had a long independent history and may possibly prove to represent a separate line of evolution from thecodont ancestors.

Flying reptiles.—While the archosaurians did not succeed in an invasion of the sea, in the air they had better success, for they not only gave rise to the birds but produced within their ranks a second aerial type—the flying reptiles of the order Pterosauria. These curious forms flourished greatly in the Jurassic, and some large types survived to late Cretaceous times. Although there presumably were pterosaurs on the continents, practically all known remains have been found in salt-water deposits, suggesting a fish-catching mode of life somewhat like that of terns today.

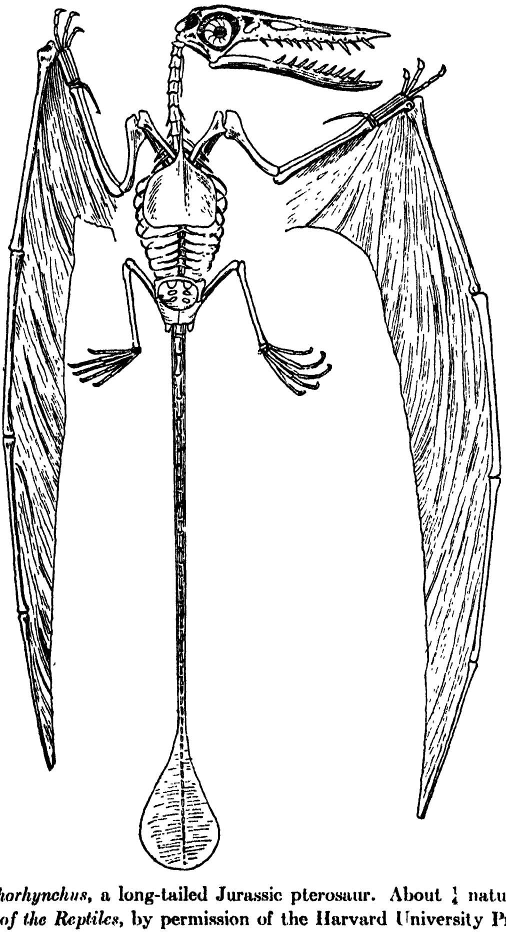


FIG. 183.—*Rhamphorhynchus*, a long-tailed Jurassic pterosaur. About ¼ natural size. (From Williston's *The Osteology of the Reptiles*, by permission of the Harvard University Press.)

The structure of the pterosaurs may perhaps be best appreciated by taking as a type the fairly representative, but rather primitive, Jurassic form, *Rhamphorhynchus* (Figs. 183, 184). This little reptile was about a foot and a half in length, with a long skull, a short body, a long tail, and, as the most striking feature, the development of the arms into elongate wings. Specimens found in sediments which preserve many delicate structures show no trace of scales (or of feathers); small hairlike structures have been described, however. The wings were composed of a membrane of skin, as in the bats, but supported only by an attachment to a single elongated finger.

Skeleton.—The head (Fig. 184) was typically archosaurian in structure, although (as in birds) the bones tended to be fused together and the sutures obscured. There were two temporal openings, below which the quadrates slanted forward so that the jaw articulation lay below the eyes. The orbits were large; the nostrils were situated well back on the long beak; the teeth were sharp and pointed. These forms appear to have been fish-eaters; *Rhamphorhynchus* was peculiar in that the teeth sloped forward rather than backward as in most carnivorous reptiles. The neck was elongated and the cervical ribs small, giving the head great freedom of motion; the trunk, on the other hand, was very short, with only ten or so dorsal segments; there was a long sacral region of more than half-a-dozen vertebrae and an elongate tail. This last structure was stiffened by strong ligaments and, as we know from impressions, bore a small steering rudder of skin.

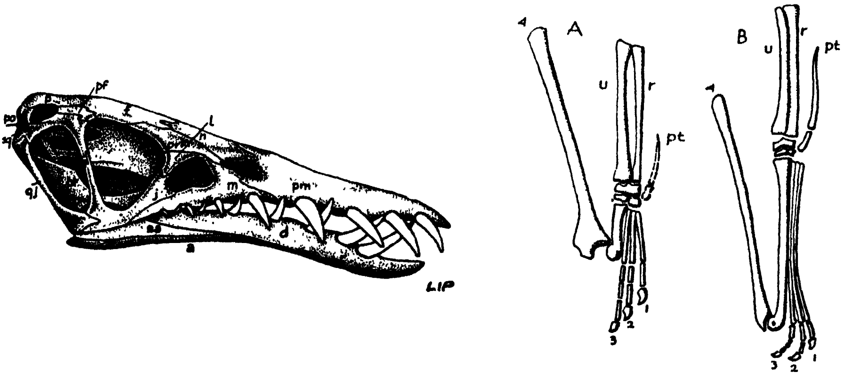


Fig. 184.—*Left*, the skull of the pterosaur *Rhamphorhynchus*; length of originals about 5 inches. For abbreviations see Figure 96. (After Jaekel.) *Right*, forearm and manus of pterosaurs. *A*, *Rhamphorhynchus*; *B*, *Pterodactylus*. The distal digits of the wing finger are omitted. Abbreviations: *pt*, elements supporting the membrane between arm and neck; *r*, radius; *u*, ulna; 1–4, first to fourth digits. (After Williston.)

The limbs were, of course, highly modified, the "arms" particularly so; many of the bones were hollow and air-filled, as in birds, thus decreasing the weight. There was a very large sternum on the ventral surface of the chest from which arose (as in birds) the main muscles having to do with wing movements. The dermal shoulder elements were absent, but scapula and coracoid were well developed. The shoulder girdle was, of course, subject to considerable stress during flight and, in this group, tended to be better attached to the body than is usually the case; not only was the bottom of the coracoid propped against the edge of the sternum, but in some pterosaurs (cf. Fig. 185) the upper edge of the scapula fitted into a notch on the side of a fused series of dorsal vertebrae.

The humerus was short and powerful, usually with a large process for the attachment of breast muscles, the radius and ulna long and placed close together. The carpus (Fig. 184) was much shortened and reduced and apparently without much motion in it; there was attached at its front edge a small, splintlike pteroid bone which seems to have supported a span of skin running up onto the neck. There is no trace of a fifth finger. The other four metacarpals ran out close together to the bases of the fingers. Three of the fingers were short but with the normal number of joints and bore small claws at their ends. The fourth finger, however, was enormously elongated with four long phalanges; this fourth finger formed the entire support for the wing membrane, which ran back to attach along the side of the body and the thigh.

The pelvic limb was also peculiar in structure. There was the usual long ilium of archosaurs, tightly attached to the numerous sacral ribs (cf. Fig. 174, *C, upper row*). Below lay a large plate which is sometimes thought to represent not only the ischium but the pubis as well. However, anterior to this there was attached a T-shaped element which met its fellow in the midline. This is thought by some to have been an extra element, a prepubis; by others it is considered to be the pubis itself. The hind legs were moderately long but slim and so articulated that it would have been difficult for the animal to walk on them in any ordinary manner.

Flight.—Obviously, flight was the normal mode of locomotion; wing membranes are perfectly preserved in a number of specimens. The action of the wings, however, must have been considerably poorer mechanically than in birds. These structures were supported only by one elongate finger; and, since the membrane was probably fairly soft, no partial movements could have been accomplished but merely a flapping of the whole structure. It seems highly probable that these forms did not move the wings so much as does the average bird but relied more upon a soaring flight for their progression. An obvious fault in construction appears to lie in the fact that, without internal supports in the wing membrane, any break or tear would have ruined the whole wing structure. This is in contrast to birds, in which a few feathers may be lost without serious results, and to bats, in which several fingers are inserted in the membrane.

It is difficult to see how pterosaurs might have got about when not in flight. Older restorations show them walking about on all fours with the wings turned back and the three small front toes on the ground, but the structure of the hind legs makes such a pose almost impossible. A bipedal mode of progression is out of the question. It seems obvious that the small front fingers were used for clutching, and the animals may have rested hanging from a limb or a rock ledge. Perhaps, as in bats, the body may have been suspended upside down from a branch, in which case the hind legs would have made good clutching organs. But it seems difficult to believe that "emergency landings" would never have been necessary; and how the animal could get itself into the air again from level ground is difficult to understand.

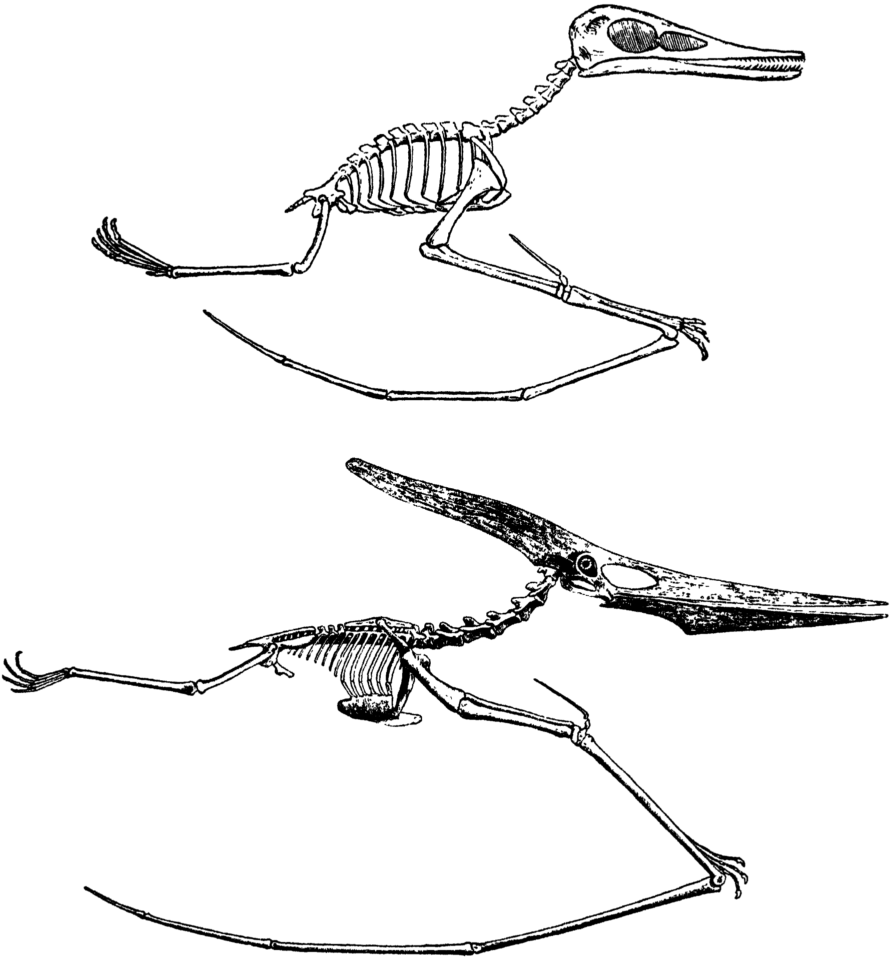


FIG. 185.—*Above*, *Pterodactylus*, a small, short-tailed Jurassic pterosaur. (From Williston's *The Osteology of the Reptiles*, by permission of the Harvard University Press.) *Below*, *Pteranodon*, a giant Cretaceous flying reptile; maximum wing spread about 27 feet. (From Eaton.)

The brain of the pterosaurs has been revealed by casts. The cerebral hemispheres are large for a reptile; very prominent are the regions which have to do with sight, while the olfactory areas are negligible, suggesting that, as in the birds, sight was all important and smell almost lost. The many other analogies with birds and the real relationship of the two groups within the archosaurian stock suggest that perhaps other bird characters may have been present. These forms quite probably were somewhat warm blooded, for it seems very necessary that there should have been a continual supply of energy for flying; and it is not impossible that the "improvements" in the circulatory system found in birds may have been present here (they are foreshadowed in the crocodiles, the only living archosaurians).

Rhamphorhynchoids.—The pterosaurs are divided into two suborders—the Rhamphorhynchoidea and Pterodactyloidea. The former, of which *Rhamphorhynchus* is typical, is the more primitive group, exclusively Jurassic in age and including the only pterosaurs known from the early part of that period (there are no known Triassic forms). Its members agree in a number of primitive features. The originally long reptilian tail was still present; teeth were usually well developed; the metacarpals in the wing were comparatively short (Fig. 184, *A*); the last toe in the foot was unreduced; and the fibula was present, although small.

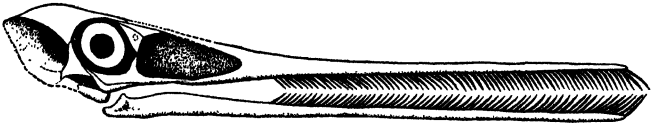


FIG. 186.—*Ctenochasma*, a Jurassic pterodactyloid pterosaur with long jaws armed with numerous slender teeth; length about 6 inches. (After Broili.)

Pterodactyloids.—But in the Jurassic there had already appeared a second, derived group—the pterodactyloids. *Pterodactylus* (Fig. 185) was a small form, some specimens being no bigger than a sparrow. The most prominent difference from the primitive types lay in the fact that there was but a stub remaining of the originally long tail. The fifth toe in the hind leg was reduced; the wing metacarpals were much elongated (Fig. 184, *B*). The dentition was much modified, and the teeth are more slender and delicate structures. In the related genus, *Ctenochasma* (Fig. 186), they are exceedingly numerous and bristle-like in appearance, suggesting the straining devices found in the bill of certain ducks. In *Pterodactylus* itself the teeth tended to be lost from the back part of the mouth at least and presumably were succeeded by a horny beak. These little pterodactyls appear to have been common along the Jurassic shores. In the Cretaceous only a few forms survived, but among them were remarkable types. The size tended to increase, and the skull tended to elongate and to develop a crest extending back from the occipital region. Teeth were entirely lost. The culmination of these tendencies is seen in *Pteranodon* (Fig. 185) of the Upper Cretaceous of Kansas, a form with a wingspread of as much as 25 feet; a long, toothless beak; and a crest nearly as long as the main part of the skull and extending back from the head.

This was the end of the pterosaurs; the group became extinct before the close of the Cretaceous.

Pterosaur history.—The structure of these forms clearly indicates that they were derived, as were other archosaurians, from some member of the Thecodontia in which a bipedal gait had been evolved. The arms were freed from the necessity of functioning in terrestrial locomotion and were available to take up other employment. Possibly, the Triassic ancestors of the pterosaurs were small climbing types; and a membrane may have developed, as in a number of other tree-dwelling vertebrates, as an aid in planing from tree to tree and breaking the fall on landing. The fifth finger was often reduced in archosaurians; and the fourth—the longest of the series—was well adapted, after the loss of the claw joint, to support a wing membrane. Why, however, the loss of ordinary walking powers should have taken place is not clear. Some light may be shed on this and other problems if ever the missing connecting types, which must have been present in the Triassic, are found as fossils.

It seems obvious that these forms were not so well adapted for a flying existence as the birds. The feathered structure of the bird's wing seems much better than the pterosaur membrane. The pterosaurs appeared first in the field; for, when the first primitive birds appeared in the Jurassic, the flying reptiles were at their peak. But, by Upper Cretaceous times, highly developed flying birds had been evolved; competition with them may have been a factor in the elimination of the last of the pterosaurs.

CHAPTER 12

DINOSAURS

MOST interesting of ruling reptiles, and perhaps the most spectacular animals of any age, were the dinosaurs. Springing from the primitive thecodont stock in the Triassic, dinosaurs were already abundant by the end of that period and were the dominant land types during the remainder of the Mesozoic. Among their numbers is included almost every large terrestrial vertebrate of the Jurassic and Cretaceous.

The popular conception of the dinosaurs is that of a single group of large reptiles. This is, however, inaccurate. Most dinosaurs were large—some reaching a weight of 40 or 50 tons—but some true dinosaurs bulked no larger than a rooster. Further, the dinosaurs were not a single group but were already divided at their first appearance into two distinct stocks, related only in that both were archosaurs descended from the primitive ruling reptiles, the Thecodontia. The term "dinosaur" is thus one which can be used only in a popular sense; scientifically the dinosaurs are arrayed in two separate orders, defined below.

Certain of the dinosaurs were carnivores, as had been their thecodont ancestors; a majority, however, abandoned this mode of life and became herbivores. All the earlier and more primitive members of both orders were bipeds, as were the more advanced thecodonts from which they had sprung. Although a majority remained bipedal until the end of dinosaurian history, many herbivorous forms in both orders reverted to a four-footed gait. But even if we know nothing of the pedigree of such quadrupedal forms, many features of their limb construction would tell us of their descent from bipedal ancestors.

The dinosaurs are divided into two orders, the Saurischia and the Ornithischia, both included in the subclass Archosauria but no more closely related to one another than to the other members or descendants of the ruling reptile group—the crocodiles, pterosaurs, and birds. The distinctions between the two dinosaurian orders were clean-cut from the first. A key character (to which the names refer) is that, while the Saurischia have the triradiate pelvic structure (Fig. 187*A*,*B*) developed in many thecodonts, the primitive Ornithischia have a two-pronged pubis, resulting in a tetraradiate type of pelvis (Fig. 187 C,E). The saurischians were primitively carnivores and all carnivorous dinosaurs pertain to that order. Some saurischians, however, became four-footed plant-eaters and developed into great amphibious forms, among which are the largest of all reptiles. The ornithischians, on the other hand, were herbivorous from the first. Many of them remained bipeds; the well-known duck-billed dinosaurs of the Cretaceous are end-forms of this line. But in this order also there was reversion to a quadrupedal gait in various armored types and the horned dinosaurs of the Cretaceous.

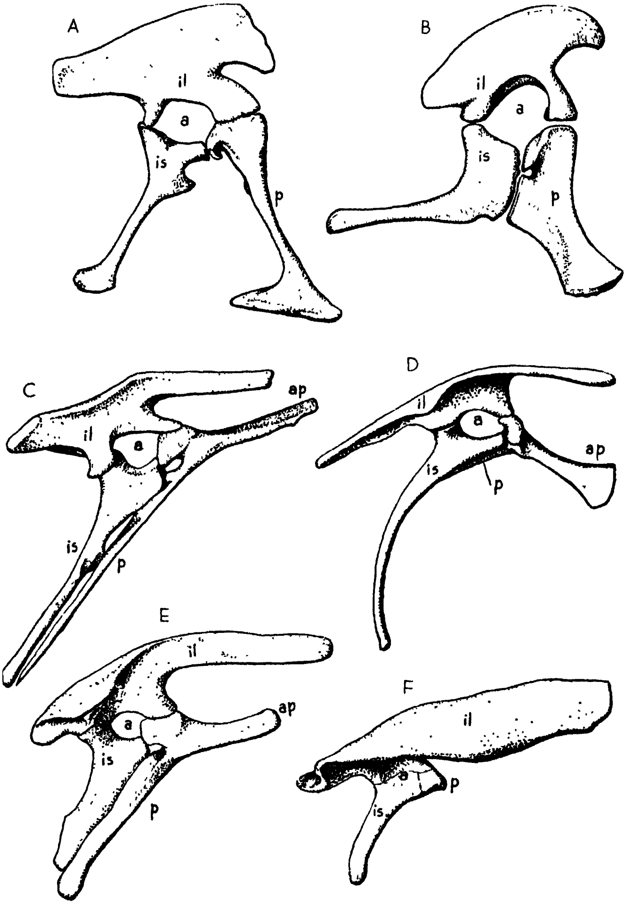


Fig. 187.—The pelvis in dinosaurs: *A*, *B*, saurischians; *C–F*, ornithischians. *A*, The theropod *Allosaurus; B*, the sauropod *Camarasaurus; C*, *Thescelosaurus*, a primitive ornithopod; *D*, *Monoclonius*, a horned dinosaur; *E*, *Stegosaurus; F*, *Ankylosaurus*, a Cretaceous armored form. Abbreviations: *a*, acetabulum; *ap*, anterior process of pubis; *il*, ilium; *is*, ischium; *p*, pubis. (*A*, *E* after Gilmore; *B* after Marsh; *D*, *F* after Brown.)

Saurischians.—The order Saurischia perhaps merits first consideration, since many of its members were still exceedingly close in structure to the small bipedal thecodonts from which all the dinosaurs presumably sprang. The typical triradiate pelvis is present in all members of this order. A majority of the group, including all the more primitive forms, were bipedal and carnivorous. Almost all (in contrast with ornithischians) had teeth present throughout the length of the jaws. The teeth were, in general, of a simple nature, primitively sharp concial structures but compressed and knifelike in some of the carnivores and blunted in herbivorous types. In correlation with the usually carnivorous mode of life, the end-phalanges were generally compressed and curved, indicating the presence of powerful claws.

Various systematic arrangements of the order have been proposed. We shall here use a conservative classification which divides the saurischians into two suborders: the Theropoda, including all the bipedal forms, mainly carnivorous in habits; and the Sauropoda, constituting a side branch of large quadrupedal, herbivorous, and amphibious types.

Primitive theropods.—The theropods (using this term in a broad sense) include all the characteristic terrestrial reptilian carnivores of the late Triassic, Jurassic, and Cretaceous. These reptiles were flesh-eating successors to the carnivorous synapsids of the Permian and early Triassic (to be described in a later chapter) and ecologic predecessors of the carnivorous mammals of the Cenozoic. All were bipeds, with long hind legs which tended to assume a rather birdlike structure and with short front limbs in which the outer digits were usually much reduced. The numerous theropods may be divided for convenience into three infra-ordinal groups: the Coelurosauria include small, slightly built, primitive forms and their relatively unspecialized descendants; the Carnosauria, the larger flesh-eaters; the Prosauropoda, the bipedal ancestors of the sauropods.

Most primitive of saurischians were a number of small coelurosaurs of the late Triassic and Jurassic. Typical genera were *Procompsognathus* of the European Upper Triassic; the contemporary American *Podokesaurus;* and *Compsognathus* and *Ornitholestes* (Fig. 188), which occur in the late Jurassic in Europe and America, respectively. All were of small size; *Podokesaurus*, even including the long tail, was little over a yard in length; *Compsognathus* was even smaller. These little forms were obviously active, fast-running bipeds. The lightness of their build was emphasized by the fact that many of the vertebrae and limb bones were hollow and presumably (as in birds) filled with air spaces.

The skull of early theropods (Figs. 188, 189) was, in general, fairly small in comparison to the size of the body, and lightly built. In most respects the cranial structure was very similar to that of such thecodonts as *Ornithosuchus* and *Euparkeria*. Such characteristic archosaurian structures as a large antorbital opening and a fenestra on the outer side of the jaw were present both here and in later and more specialized saurischians. The thecodont (socketed) teeth were long, sharp, often somewhat compressed and recurved, and usually well adapted to a carnivorous diet.

The vertebrae were primitively amphicoelous or with flat ends on the centra (platycoelous); in Jurassic and Cretaceous saurischians, opisthocoelous vertebrae were common, particularly in the front end of the vertebral column. The backbone included about ten rather elongate cervicals, thirteen or so trunk vertebrae, usually four sacrals united with the expanded ilium, and a long, slim tail. Seemingly, the neck was held well erect, with the head bent forward at a right angle. The tail served as a balancer and (as indicated by many specimens of footprints of carnivorous dinosaurs) was held clear of the ground. In many theropods the tail was stiffened by long processes which extended forward from each prezygapophysis to interlock with the preceding vertebra. Slim ventral ribs have been found along the belly in many specimens.

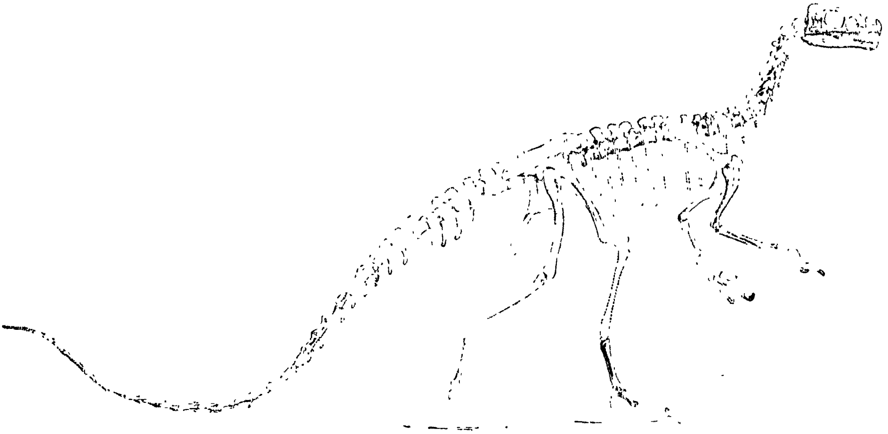


FIG. 188.—*Ornitholestes*, a small late Jurassic carnivorous dinosaur (coelurosaur), about 6 feet long. (From Osborn.)

The theropod pelvic girdle (Fig. 187, *A*) was of a simple triradiate pattern. The pubis was presumably rather broad in the most primitive theropod ancestors but generally had the form of a long, slim rod somewhat dilated distally, and the ischium was similarly elongated. The acetabulum was widely perforated to receive the head of the femur, in contrast to the solid build of this area in most reptiles; this is one of the few characters by which the early theropods can be distinguished from their more primitive thecodont relatives. The hind legs were long and slim and presumably were restricted to a straight fore-and-aft type of movement, with a high development of the adaptations for bipedal locomotion discussed in the preceding chapter. The femur in primitive theropods was generally somewhat shorter than the tibia; in life this would have resulted in the development of considerable speed, a short swift stroke of the thigh muscles being accompanied by a long swing of the tibia (in slow and ponderous tetrapods the femur is long, the tibia short). In the foot (Fig. 190, *A*, *lower row*) the fifth toe (as in most archosaurs) had been reduced to a short metatarsal with, at the most, a vestigial nubbin or two representing the digits. In many theropods the first toe, as well, was considerably shortened and tended to be set off at an angle from the other three. In the second to fourth toes the metatarsals tended to be much elongated and closely appressed, and the central digit was somewhat longer than its neighbors, resulting in a very birdlike foot structure. So similar are the feet of theropods to those of their avian relatives that when numerous dinosaur footprints were discovered a century ago in the Triassic rocks of the Connecticut Valley they were thought to pertain to ancestral birds.

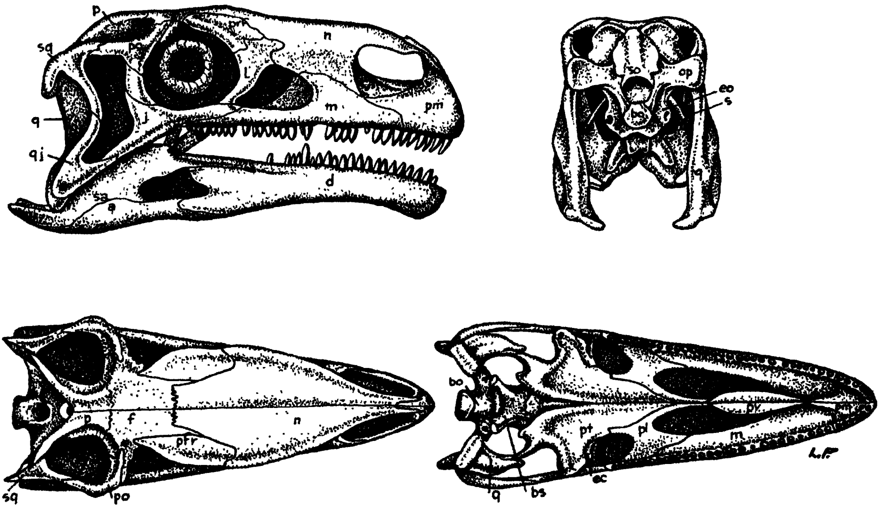


FIG. 189.—The skull of the Triassic saurischian dinosaur *Plateosaurus;* length of original about 13 inches. *pfr*, Prefrontal; *so*, supraoccipital. For other abbreviations see Figure 96. (After von Huene.)

The shoulder girdle in these and other dinosaur types (Fig. 174) consisted merely of an elongated scapula and a single rounded coracoid. Almost never is there any trace in dinosaurs of the dermal elements found in the shoulder girdle of more primitive reptiles. The front limb was much shorter than the hind. In every known form the fifth digit had been much reduced (Fig. 190, *A*, *upper row*). The remaining four fingers were all still well developed in *Procompsognathus;* but in the Jurassic genera the fourth digit was also reduced, leaving only the three inner ones functional. Presumably the front limb was used little, if at all, in supporting the body (except in a resting pose) but may have aided in feeding.

There were a number of small coelurosaurs of this general type in the latter part of the Triassic. They appear to have been not far from the ancestral thecodonts in most structural features and in some cases can scarcely be distinguished from members of that group. In the Jurassic such forms were comparatively rare and were tending to specialize in various directions. *Compsognathus,* known from a skeleton from the lithographic stone of southern Germany, is the only well-known European Jurassic type. This was a very small and lightly built dinosaur with about the bulk of a fowl. In the manus there were three well-developed digits, subequal in length, and vestiges of the two outer ones. *Ornitholestes* of the late Jurassic Morrison beds was a considerably larger reptile, with a total length of about 6 feet and a rather stouter build. Here only the three inner digits of the manus were preserved; the pollex was shorter than the others and somewhat divergent; seemingly, this form had developed a grasping type of hand. The obvious agility of this little

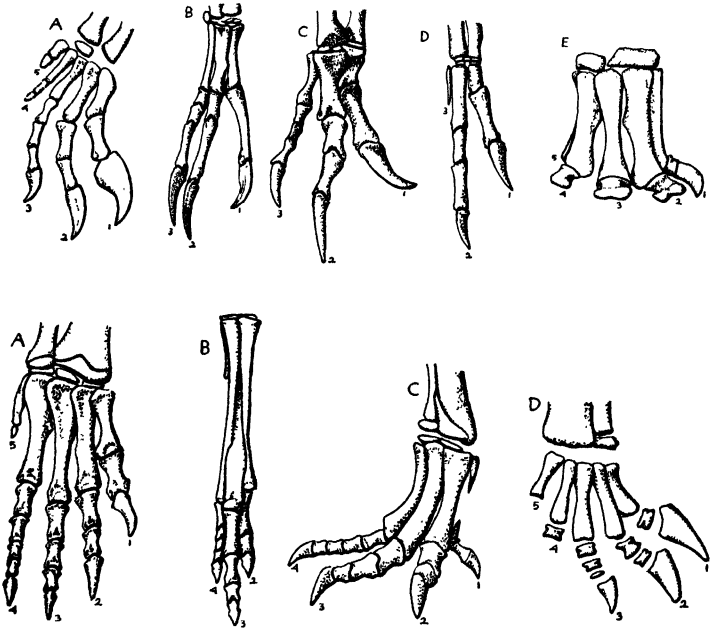


FIG. 190.—*Above,* the manus in saurischian dinosaurs: *A, Yaleosaurus* [*Anchisaurus*]; *B, Struthiomimus; C, Allosaurus; D, Gorgosaurus; E, Diplodocus.* (*A* after Marsh; *B, E* after Osborn; *C* after Gilmore; *D* after Lambe.) *Below,* the pes of saurischian dinosaurs: *A, Yaleosaurus; B, Struthiomimus; C, Allosaurus; D, Camarasaurus.* (*A* after Marsh; *B* after Osborn; *C, D* after Gilmore.)

dinosaur and the clutching power of the hand led to a belief that this form might have preyed upon the contemporary primitive birds (a suggestion preserved in the generic name). This is improbable; presumably, small reptiles such as lizards and perhaps the small early mammals may have been the staple articles of diet of this and other tiny dinosaurs.

Ostrich-like dinosaurs.—Almost no remains of such small coelurosaurs are known from Cretaceous deposits, but their descendants are to be recognized in *Ornithomimus* and *Struthiomimus* (Fig. 191) of the North American Cretaceous and related Old World contemporaries. *Struthiomimus* was about the size of an ostrich and (as the name implies) not unlike that bird in general proportions, with very long, slim hind legs, a long neck, and a small head. The foot (Fig. 190, *B*, *lower row*) was three toed and very birdlike. The three metatarsals were very long and closely appressed; the central one was much reduced proximally, its neighbors taking over most of its weight-supporting function. Despite the fact that these forms were obviously purely bipedal in habits, the front limbs were quite long. The three inner fingers were all well developed, and the first was seemingly opposable to the other

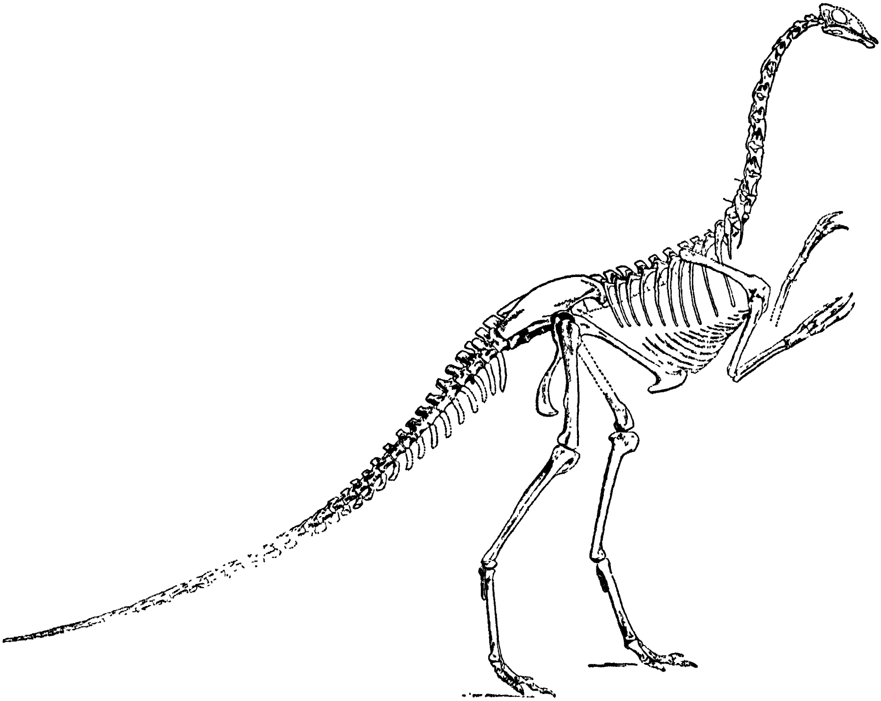


FIG. 191.—*Struthiomimus*, an ostrich-like Cretaceous saurischian dinosaur, about 5 feet in height. (From Osborn.)

two, forming an effective grasping organ (Fig. 190, *B*, *upper row*). The skull was quite small and very lightly built, with a superficially birdlike appearance. This resemblance is greatly heightened through the fact that, almost alone among dinosaurs, *Struthiomimus* and its relatives had entirely lost their teeth and presumably had replaced them functionally with a horny bill. The jaws were short and weak.

The odd combination of specializations found in these ostrich-like forms—great swiftness, a grasping ability in the well-developed "hands," and the weak and toothless jaws—has caused considerable discussion as to their mode of life. The happiest idea put forward was that these forms made a living by robbing eggs from the nests of other dinosaurs. Teeth are unnecessary for egg-eating, and the shell can be effectively broken with a horny beak; the "hands" would be of great use in handling the eggs; and the speed was necessary to escape the enraged parents! As if in confirmation of this suggestion came the subsequent discovery in Mongolia of a crushed skull of an ostrich-like dinosaur in a nest of fossil eggs belonging to a dinosaur of a different group. It would almost seem as if this reptile had actually been caught in the act of egg-stealing.

Larger carnivorous types.—While the ancestral theropods were presumably small forms, such as those described above, more powerful carnivores—the Carnosauria—began to make their appearance at an early date. A number of carnivores with a much larger size and a heavier build have been described from the Upper Triassic of South Africa, and there are numerous footprints (but unfortunately few adequate skeletal remains) of other large dinosaurs in beds of that age in Europe and North America. Many of these types are probable ancestors of the sauropods. However, *Teratosaurus* [*Zanclodon*], a large form from the Triassic of Europe which is incompletely known, was distinguished from most of its contemporaries by the possession of a skull very large in proportion to its body and by large, compressed, and recurved teeth. It is from some such form that there arose the large flesh-eating dinosaurs of the Jurassic.

There are numerous scattered finds, in European deposits representing nearly every stage of the Jurassic, to which the generic term *Megalosaurus* is usually applied. Most of these remains are, however, fragmentary and tell us little beyond the fact that large flesh-eaters were abroad in the land. Well-preserved specimens of large Jurassic carnivores are found only in the Morrison beds of North America; from these beds have been obtained nearly complete skeletons of *Allosaurus* and *Ceratosaurus*.

Allosaurus was an animal with a total length of about 34 feet; it was seemingly powerful enough to have attacked any of its herbivorous contemporaries, even the giant sauropods. The skull (Fig. 192), in contrast with that of most smaller or earlier theropods, was quite large in proportion to the body;

the teeth were large and sharp, the jaws long and deep. A curious feature is found in the fact that the quadrate was loosely united to the other skull elements, and there appears also to have been some possibility of movement between the frontal and the parietal bones. Apparently, this was an adaptation for bolting large masses of flesh—a type of structural modification which we have seen carried to an extreme in the snakes and which is also present to some extent in birds.

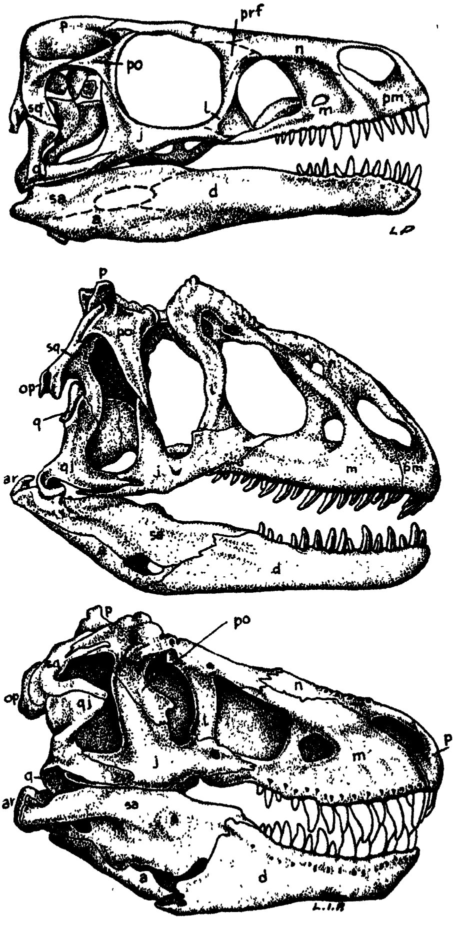


FIG. 192.—The skull of carnivorous theropods. *Above, Ornitholestes,* a small Jurassic coelurosaur, the braincase imperfect; original about 5 inches long. (After Osborn.) *Center, Allosaurus,* a large late Jurassic carnosaur; length of original about 27 inches. (After Gilmore.) *Below, Tyrannosaurus,* a late Cretaceous carnosaur; skull length about 50 inches. (After Osborn.) For abbreviations see Figure 96.

The body was rather massively built. The neck vertebrae were opisthocoelous, and extra articulations, in addition to the normal zygapophyses, tended to add to the strength of the backbone. The hind legs, in correlation with the size of the creature, were stout and only moderately long, and the femur was somewhat longer than the tibia. The metatarsals were rather short, but otherwise the foot (Fig. 190, *C, lower row*) was quite birdlike, with three well-developed toes and a small first toe turned backward as a prop, much as in many avian types. The front limb was short but fairly stoutly built, with three spreading, claw-tipped digits (Fig. 190, *C, upper row*); it was obviously not a supporting structure but may have been of considerable use in feeding.

Ceratosaurus was a somewhat smaller type in which the most striking feature was the development of a small median horn on the nasal bones. There was a somewhat more progressive condition in the feet of this form, for all three metatarsals had partly fused to form a single solid bone. This is parallel to the development seen in birds, in which these elements have fused completely; but the process of fusion was carried no further in any known dinosaur. The front foot of *Ceratosaurus* was, on the contrary, comparatively primitive, for there was little reduction of the outer two digits.

Little is known of the carnivores of the early Cretaceous, and it is doubtful whether the Jurassic carnosaurs gave rise to the typical large carnivores of the later part of that period. From them, however, may have been derived *Spinosaurus* of the Cretaceous of Egypt. This large flesh-eater is poorly known but was remarkable in that the neural spines were greatly elongated, rather after the fashion of some of the Permian pelycosaurs described in a later chapter; some spines had a length of about 6 feet.

Cretaceous carnivores.—The characteristic carnosaurs of the late Cretaceous were the still larger and more powerful deinodonts, of which *Tyrannosaurus* (Fig. 192), *Deinodon*, and *Gorgosaurus* (Fig. 193) of western North America are the best-known forms. *Tyrannosaurus* reached a length of some 47 feet and stood about 19 feet high in walking pose, while *Deinodon* was nearly as large. These reptiles were the largest terrestrial flesh-eaters known from any period in the history of the world. The body was heavy in its construction, and the hind legs were massively built. The metatarsals were moderately elongated, and (as in the contemporary ornithomimids) the middle one was much reduced in size. The front legs were absurdly small and weak and seem to have been practically useless; they were too short to reach the mouth and seemingly too weak to have been of any assistance in seizing or rending the prey. Only two small digits were present in *Gorgosaurus* (Fig. 190, *D*, *upper row*), and probably the same was true in *Tyrannosaurus*.

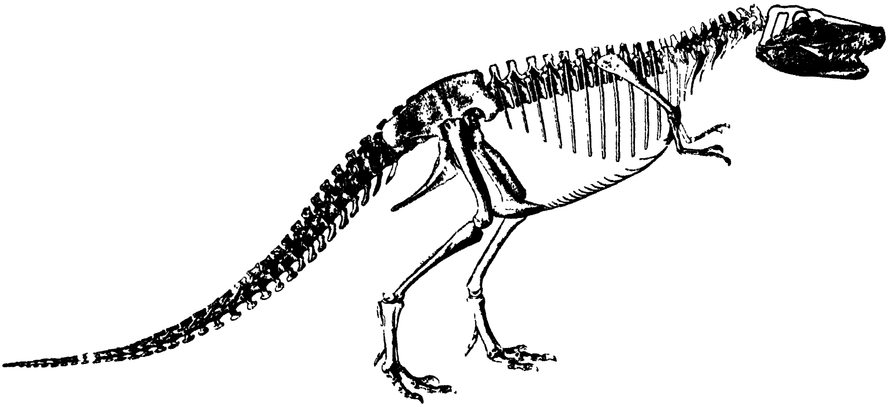


FIG. 193.—*Gorgosaurus*, a gigantic Cretaceous theropod dinosaur; length about 29 feet. (From Lambe.)

The skull was very large and massively built, with the fenestrae of small size. The jaws were armed with powerful teeth, some half a foot in length, recurved, and with serrate edges. The cervical vertebrae, which bore the weight of the heavy head, were short and broad.

These forms, although agreeing with the megalosaurs in many adaptive features, are thought by some not to be their descendants. Certain structural features, such as the metatarsal construction mentioned above, suggest that they represent a parallel development from the primitive stock of small bipeds. Some comparatively small deinodonts (one with a skull only 8 inches long) from the Upper Cretaceous seem to be rather primitive in character and may represent transitional types.

The reign of the deinodonts was a brief one, for they disappeared at the end of the Cretaceous. Their extinction was obviously consequent upon the extermination of the herbivorous dinosaur types, which presumably formed their food supply.

Sauropod ancestors.—We have still to consider the history of the sauropods—Jurassic and Cretaceous saurischians which became herbivores, reverted to a quadrupedal pose, and reached gigantic proportions. The ancestors of these forms are unquestionably to be sought among the larger Triassic theropods which may appropriately be termed the Prosauropoda.

A first step in sauropod development is perhaps illustrated by *Yaleosaurus* [*Anchisaurus*] of the Upper Triassic of North America. This was a small dinosaur (the largest specimen was but 7 or 8 feet long), and many of the bones were still hollow in coelurosaur fashion. There are many suggestions, however, of sauropod relationships. The teeth were comparatively blunt and straight; and the jaw was short, the quadrate slanting forward as well as down to reach the jaw articulation; these are sauropod features. Highly suggestive is the persistently primitive construction of the limbs. Despite the small size of this animal, the hind legs were comparatively short and clumsy and the metapodials were not greatly elongated (Fig. 190, *A*, *lower row*). While the fifth toe had been reduced, the other four were all well developed; and the hallux was not, as in the majority of carnivores, turned back and separated from the three middle digits. The front legs were comparatively little shortened; they were still about two-thirds the length of the hind limbs and were stoutly built. The fifth digit in the hand (Fig. 190, *A*, *top row*) was considerably reduced, and the fourth reduced to some extent as well. Probably these forms were not purely bipedal in habits and retained the possibility of walking on all fours.

Farther along the line toward the sauropods was *Plateosaurus* (Figs. 189, 194) of the Upper Triassic of Germany, a much larger form, of which complete skeletons with a length of as much as 20 feet are known. The build of the body was quite clumsy and ponderous, with much the same set of structural features as those found in *Yaleosaurus*. The head was very small in proportion to the bulk of the body, as in the sauropods themselves.

Sauropods.—From such types seem to have descended the sauropods of the Jurassic and Cretaceous, a series of forms which include not only the largest of all reptiles but the largest four-footed animals of any time. Among the better-known sauropods are *Apatosaurus* [*Brontosaurus*], *Diplodocus* (Figs. 195, 196), and *Camarasaurus* (Figs. 195, 196)—forms whose remains are among the most spectacular attractions of many museums.

The most obvious contrasts between the sauropods and their carnivorous relatives lie in the quadrupedal pose of the body and in the bodily proportions. The sauropods were massively built, with powerful limbs (the front ones almost always considerably the shorter), a long tail, and a long neck terminating in a small head.

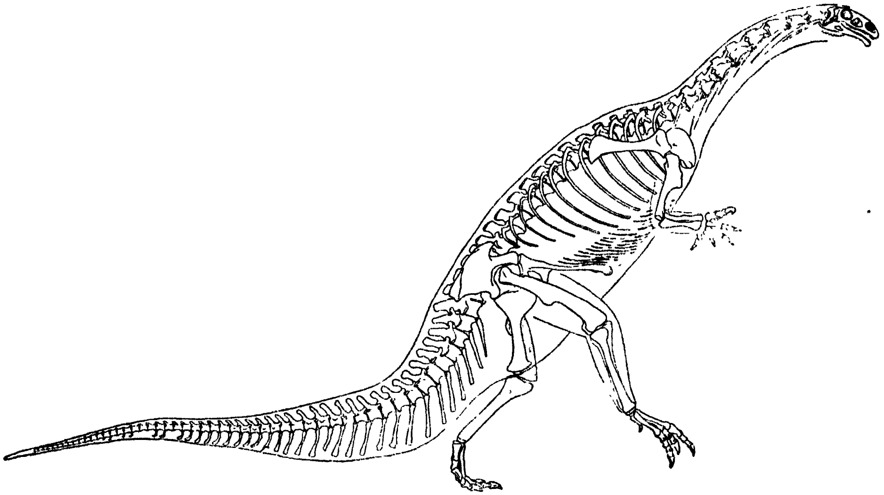


Fig. 194.—*Plateosaurus*, a Triassic ancestor of the sauropod dinosaurs; length about 21 feet. (From von Huene.)

The skull (Fig. 196) in sauropods seems absurdly small in proportion to the size of the animal. It was generally quite lightly built, with large temporal fenestrae and a large antorbital opening (there was a second smaller one in *Diplodocus*). The orbits were of good size and were situated high up on the side of the head. In *Camarasaurus* the external nares were very large and reached high up on the short skull; in *Diplodocus* the two openings were fused and situated at the top of the skull between the eyes. The position of these organs, analogous to that in many water-living tetrapods, suggests an amphibious mode of life for the sauropods; the animal could breathe and look about with only the top of the head exposed above the water.

The jaws were short and weak, the quadrate slanting downward and forward to the jaw articulation. The teeth were small and slim, peglike or spoon-

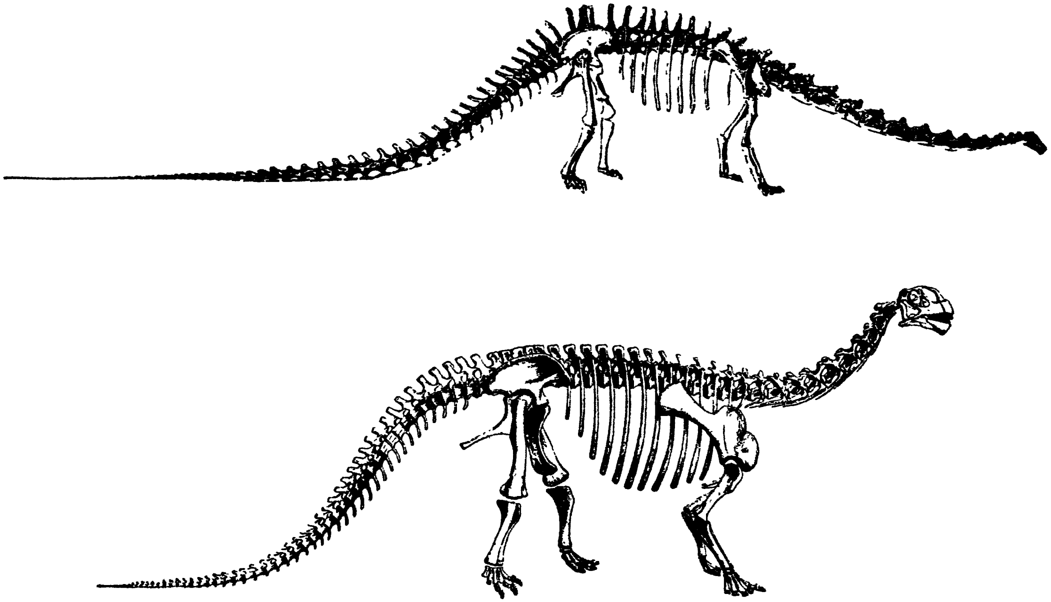


Fig. 195.—The skeleton of sauropods. *Above, Diplodocus*, lengthiest of late Jurassic sauropod dinosaurs (87½ feet). (From Holland.) *Below, Camarasaurus*, a comparatively small late Jurassic sauropod dinosaur; original of figure about 18½ feet long. (From Gilmore.)

shaped; there were seldom more than a dozen or so in each jaw half. It seems almost impossible that this dental and jaw apparatus could have been capable of cropping enough fodder to supply such a huge body, although the food material may have been some soft type of water vegetation which could be eaten with little effort.

The brain was small in size in all dinosaurs but excessively so, proportionately, in the sauropods, in which the endocranial cavity was but a small recess in the posterior part of the small skull. Presumably the brain had few functions other than working the jaws, receiving sensory impressions, and passing the news back down the spinal cord to the pelvic region, from which originated the nerves working the hind legs. Here there was situated an enlargement of the spinal cord several times as big as the entire brain.

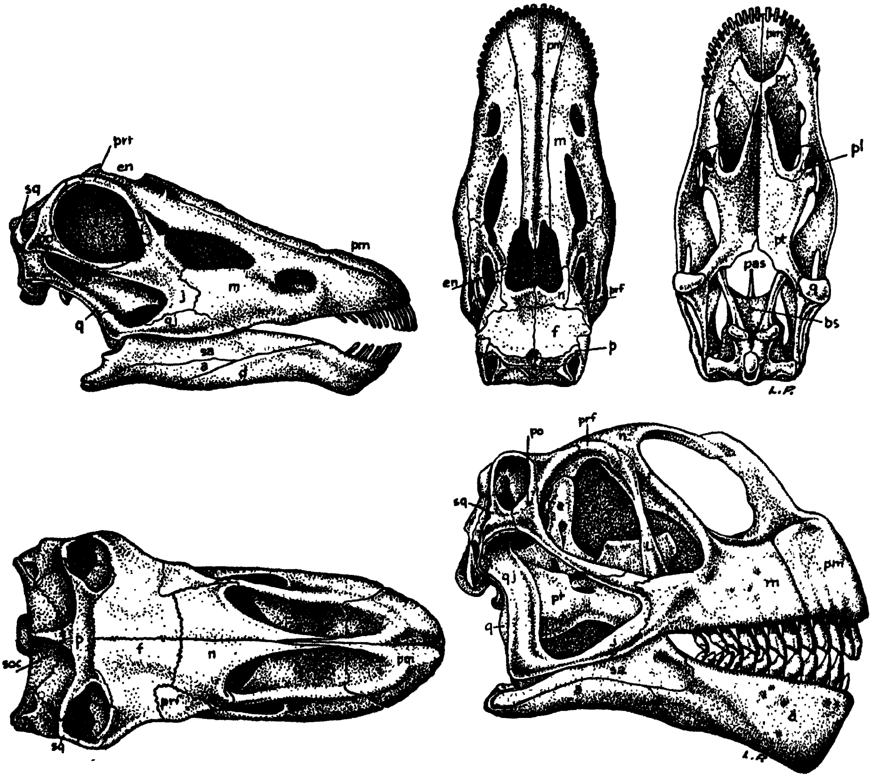


FIG. 196.—The skull of sauropods. *Above, Diplodocus*, lateral, dorsal, and palatal views; length about 2 feet. (After Holland.) *Below, Camarasaurus*, length about 1 foot. (After Gilmore.) *pas*, Parasphenoid. For other abbreviations see Figure 96.

A monumental construction of the backbone was required to carry the weight of the enormous body and transfer it to the legs. The anterior vertebrae, which had only the tiny head to support, were small; but in the trunk the centra of the vertebrae become progressively massive as we pass up over the arch of the back to the hip region. The neural spines, low in front, increase rapidly in height and reach a maximum at the top of the arch just in front of the pelvis. Presumably an interlacing series of ligaments and tendons passed between these spines and helped to strengthen the back. In many sauropods the neural spines of the anterior vertebrae were cleft at their upper ends, and probably a stout longitudinal ligament lay between the two prongs.

But the dead weight of the backbone itself was a great burden; in correlation with this we find that adaptations had developed which greatly decreased the weight of the vertebrae (Fig. 197). These structures were generally cavernous; great areas were hollowed out at the sides of the centra and arches; these were presumably filled with air sacs connecting, as in birds, with the lungs. Weight was thus much reduced, but all the essential framework of the vertebrae was left intact.

The pelvic elements (Fig. 187, *B*) were short but stoutly constructed; the ventral elements had more of the primitive platelike aspect than was the case in most theropods. The hind-limb bones were massive, with the femur considerably longer than the tibia; presumably the limbs extended straight down from the body in elephantine fashion. The front legs were generally much shorter than the hind, a feature suggestive of the probable bipedal ancestry of the sauropods. They bore less of the weight than the hind limbs and may have been less straight, the elbows projecting somewhat. In both front and hind feet (Fig. 190) the metapodials and phalanges were short, stout, and spreading; footprints show that the limbs terminated, as in elephants, in a broad pad in which the toes were incased. The details of foot construction are poorly known in most cases, but from one to three of the digits in each foot bore a large projecting claw, which presumably was of use in preventing slipping.

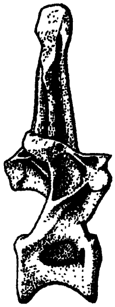


FIG. 197.—A dorsal vertebra of the sauropod dinosaur *Diplodocus*. (After Hatcher.)

The pose of sauropod limbs has been a much debated subject. It has been argued that, since in most reptiles the femur projects sideways from the body, the sauropods, too, should be mounted in this fashion. As a matter of fact, this cannot be done without doing violence to the articular surfaces of the bones. But, more than this, it would have been impossible for the animal to have supported an enormous weight with any type of limb other than a straight column. With the limbs sprawled sideways, no mere muscles could have withstood the direct pull of the score or more of tons that the hind legs of a big sauropod had to support; the animal would have sagged to the ground.

But, even granting the columnar position of the legs, it is difficult to see how these dinosaurs ever walked on land; the elements of physics show that there are natural limits to the possible size of a four-footed vertebrate. An elephant does not and cannot have the slim limbs of a gazelle; *Deinodon* and *Tyrannosaurus* could not have the slender hind legs of the little coëlurosaurs. The weight of an animal varies in proportion to the cube of a linear dimension. But the strength of a leg, like that of any structural supporting element, is proportionate to its cross-section, which increases only by squares. If a reptile doubles his length, his weight is approximately eight times as great, but his legs are but four times as strong. Hence in large animals the bulk of the legs must increase out of all proportion to the rest of the body. The legs of sauropods were large, but, even so, it seems doubtful whether they could have borne so many tons of weight. For this reason, as well as because of cranial features noted earlier, it appears probable that the sauropods were amphibious types which spent most of their lives in lowland swamps and lagoons, where they were buoyed up by the water, and problems of support and locomotion were greatly simplified.

Sauropods are unknown in the Triassic, although we have noted some seemingly ancestral types, and some later Triassic South African forms appear to have been even closer to the sauropod condition. In the older part of the Jurassic there are fragmentary remains, particularly in Europe, to most of which the name *Cetiosaurus* has been applied. In the Morrison beds of North America and beds of similar age in East Africa have been found a considerable number of well-preserved specimens of a variety of sauropod types. *Camarasaurus* of North America was a comparatively small and unspecialized form. *Apatosaurus* [*Brontosaurus*] was a bulkier relative, which reached a length in one specimen of some 67 feet and an estimated weight of perhaps 30 tons. *Diplodocus* was a slimly built form, which may not have been nearly so heavy as the last but which, with a whiplash at the end of his tail, reached the record for length—87½ feet. *Brachiosaurus*, known both from North America and East Africa, was the real giant of the group. The tail was comparatively short, but, even so, the body may have been close to 80 feet in length. The body was extremely stout, and (in contrast with almost all other sauropods) the front legs were long. Above the shoulders there extended a long neck which could place the head above the level of the roof of a three-story building; this build presumably was an adaptation for life in deep waters. A rough guess at the weight of this great animal would be somewhere close to 50 tons.

It is probable that sauropods were still abundant in Lower Cretaceous times, although there are relatively few fossiliferous deposits. In the Upper

Cretaceous, sauropods are rare in the northern continents; for example, only two specimens have been found in all the rich dinosaur beds of the North American deposits of that age. In India and the southern continents, however, *Titanosaurus* and related genera seem still to have flourished at this time.

The decline and final disappearance of these great reptiles may perhaps be correlated with geologic events. Their environment seems to have been a restricted one and if, as seems likely, continental elevation toward the end of the Mesozoic greatly reduced the area of the lowland swampy regions in which the sauropods dwelt, their extinction was almost inevitable; changes taking place in the vegetation at this time may also have been of great importance.

Ornithischians.—Members of the second order of dinosaurs, the Ornithischia, never reached the size attained by some of their saurischian cousins but are perhaps of even greater interest because of the variety of bizarre types into which they developed. The most characteristic feature of the order, one by which the skeletons of these forms may be told at a glance, was the tetraradiate type of pelvis (Fig. 187). The ilium and ischium were roughly comparable in shape and position to those elements in the saurischians, but the pubis was peculiarly constructed. Its main portion had not only rotated downward but also backward, so that it lay parallel to and close beside the ischium, while—presumably in relation to the need for support of the abdomen—a broad new process had developed which projected forward and outward along the margin of the belly.

The limbs in ornithischians were never so efficiently developed for bipedal locomotion as those of the theropods, and the front legs were never so much reduced or shortened as in those forms. It is probable that few ornithischians were entirely bipedal in habits; the front legs were very likely used in locomotion at times in even the most lightly built types. A great number of ornithischians, apparently representing several independent phyletic lines, reverted completely to a quadrupedal gait.

The ornithischians were, even at their earliest appearance, herbivorous forms. The teeth were generally leaf-shaped, with crenulated edges. In only a few known genera were there teeth in the front part of the mouth; in the vast majority this region was toothless and presumably covered with a horny beak. In the lower jaw the beak capped a median predentary bone, an element not found in any other reptilian group.

The Ornithischia may be divided into the following suborders: (1) Ornithopoda, bipedal forms; (2) the Stegosauria, quadrupedal forms with a double row of protective plates and spines down the back and tail; (3) the Ankylosauria, heavily armored, rather turtle-like quadrupeds; and (4) the Ceratopsia, horned dinosaurs.

Primitive ornithopods.—*Camptosaurus* (Fig. 198), common in the late Jurassic and early Cretaceous of Europe and North America, may be used as a basis for the consideration of the ornithopods, the most primitive of ornithischian suborders; some of its contemporaries and predecessors were smaller and somewhat more primitive in structure but are less adequately known. Various specimens of this genus show a range in length of from 7 to 17 feet.

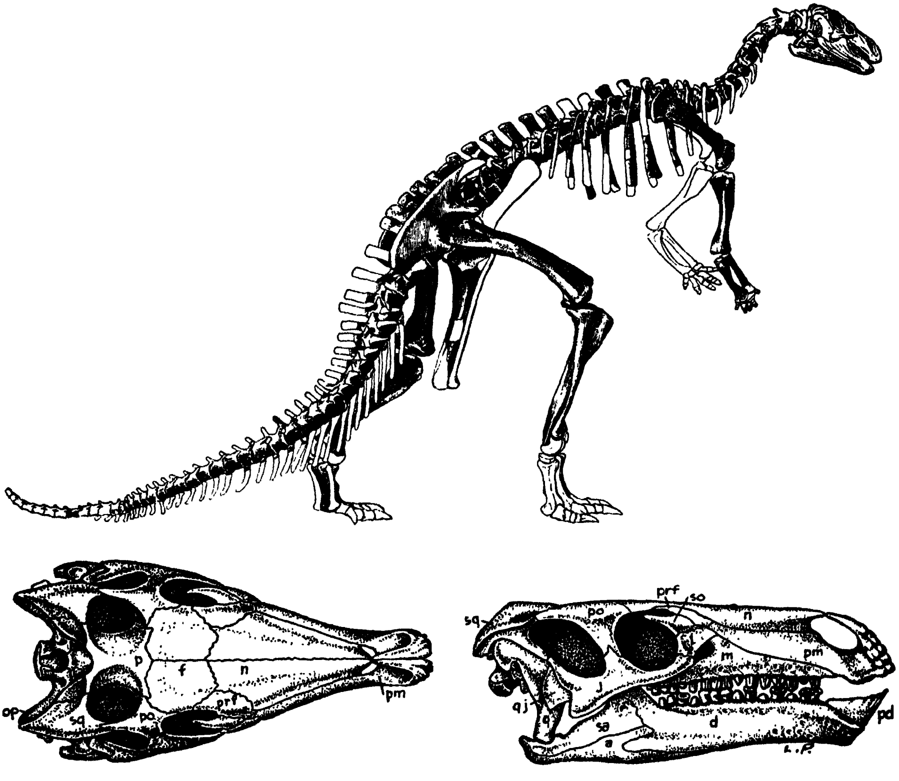


FIG. 198.—*Camptosaurus*, a Jurassic ornithopod. *Above*, the skeleton. *Below*, dorsal and lateral views of the skull; length about 16 inches. For abbreviations see Figure 96. (After Gilmore.)

The skull was long and low and, as compared with saurischians of similar dimensions, rather heavy in its construction. An antorbital opening was present but was of small size. The external nares were oval openings much larger than those of most reptiles and were nearly completely surrounded by the enlarged premaxillae; the nasals, which bounded them above, were also elongated and stretched back along the top of the skull to the level of the orbits. An extra element, a supraorbital bone, lay in the upper anterior margin of the orbit.

As in sauropods (but in contrast with carnivorous dinosaurs), the jaws were rather short and did not reach the full length of the skull. The lower jaw was heavily built; and a powerful musculature is suggested by the fact that a coronoid process (seen elsewhere among reptiles only in placodonts and mammal-like forms) extended up beneath the edge of the cheek region of the skull for the attachment of the temporal muscles, while a process projecting back from the articular region was developed for the muscles opening the jaws. There was a well-developed predentary bone in the lower jaw. The front part of the mouth was toothless and presumably covered by a horny beak; the teeth were confined to a single row in the cheek region. Teeth, however, were still present in the premaxillary region in a smaller contemporary.

The normal position of the body was presumably the bipedal one, with the neck well erect, for the occipital condyle of the skull projected downward rather than backward, indicating that the head was held at right angles to the backbone. The neck vertebrae were opisthocoelous in *Camptosaurus*, as were the anterior trunk vertebrae also in many more advanced forms. The arch of the back was stiffened in ornithopods by a latticework of tendons which (particularly in the duck-billed dinosaurs) were often ossified and thus preserved in fossil specimens.

The primitive ornithopods had the typical tetraradiate type of pelvis described above (Fig. 187, *C*). The ilium was considerably lengthened; both pubis and ischium were greatly elongated and of subequal length, and the former bone had a long anterior process. The limbs in *Camptosaurus*, as in ornithopods in general, were somewhat more massive and shorter than those of saurischians of equal size; presumably in these herbivores the demand for speed was not so great as in carnivorous types. The tibia never exceeded the femur in length; and, although the ornithopods were digitigrade types, walking on their toes rather than on the flat of the foot, the metapodials were but little elongated. In primitive ornithischians, as in saurischians, the fifth toe was functionless, and the first was reduced in length (Fig. 199, *D*). Claws appear to have been present but were usually rather blunt.

The front legs were not so short as in most bipedal saurischians; in *Camptosaurus* they were about two-thirds the length of the hind limbs. All five digits were present, but in even the most primitive of known ornithischians the outer two were reduced, much as in the early theropods (Fig. 199, *A*). The terminal phalanges of the manus in *Camptosaurus* and more advanced forms were broadened and presumably were covered by small hoof-like structures rather than claws. Very probably the front legs were used for support while feeding or walking slowly.

In contrast with the saurischians, the ornithischians were rare in the early days of dinosaurian history. There are no intermediate types known which might serve to connect them with any of the better-known thecodont families. From the Triassic there is only a single fragmentary specimen which appears to pertain to the present order, and we know almost nothing of ornithischians during most of the Jurassic. A number of forms, however, appear in late Jurassic and early Cretaceous deposits in both Europe and North America.

Hypsilophodon of the Lower Cretaceous Wealden beds of Europe is among the most primitive of known ornithopods. This animal was scarcely more than a yard in length, and some structural features suggest arboreal habits comparable to those of the tree kangaroo of Australia. Teeth were still present in the premaxilla in *Hypsilophodon;* and an interesting feature is the fact that there appear to have been two rows of small bony plates running down the mid-line of the back, much as in many thecodonts. There are several other incompletely known small forms of this general type in the Morrison beds of North America and even from the Upper Cretaceous. *Camptosaurus*, as described above, was a somewhat larger and more advanced form.

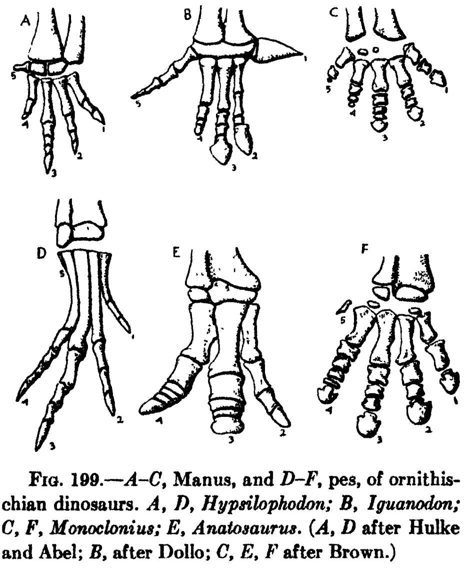


Fig. 199.—*A–C*, Manus, and *D–F*, pes, of ornithischian dinosaurs. *A*, *D*, *Hypsilophodon; B*, *Iguanodon; C*, *F*, *Monoclonius; E*, *Anatosaurus*. (*A*, *D* after Hulke and Abel; *B*, after Dollo; *C*, *E*, *F* after Brown.)

Best-known of European ornithopods is *Iguanodon* of the Wealden, a form twice the size of *Camptosaurus*. Numerous remains have been found both in England and on the Continent. The most striking of European dinosaur finds was the discovery of more than a score of individuals belonging to this genus in the process of excavation of a Belgian coal mine. Apparently, a herd of these large reptiles had fallen into a crevasse in the older Carboniferous rocks and were buried there. An interesting specialization in *Iguanodon* is that the terminal phalanx of the short "thumb" is a stout but pointed spike of bone which may have been an excellent defensive weapon (Fig. 199, *B*).

Two small bipeds from the Lower Cretaceous of Asia—*Psittacosaurus* and *Protiguanodon*—are in most respects normal ornithopods. The skull, however, has a deep and powerful beak; this and other features suggest that these genera are ancestral to the horned dinosaurs of the later Cretaceous.

A curiously aberrant group of Upper Cretaceous forms is that represented by *Troödon* (Fig. 201). In this genus the postcranial skeleton is of a normal ornithopod build, but the head is grotesque in its development. Above the jaws (with a feeble dentition) and the orbits, the skull expands upward into an enormous bony dome with a rugose surface and surrounded with an "ornamental" area of spikes and rugosities, presumably defensive in nature. The internal structure of the dome belies the intellectual appearance of the animal, for it is formed entirely of thick and solid bone. The dentition is primitive in the retention of premaxillary teeth. The skull is comparable in certain respects to that of the contemporary ankylosaurs, but the resemblance is apparently superficial only.

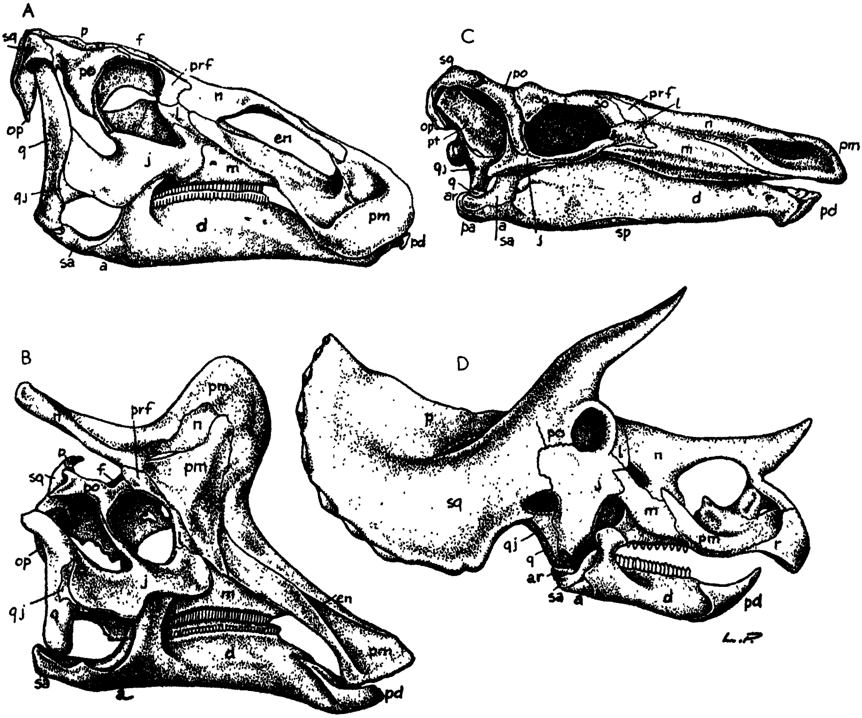


FIG. 200.—The skull in various ornithischian dinosaurs. *A*, *Edmontosaurus*, an Upper Cretaceous duck-billed ornithopod; length of skull about 3½ feet. *B*, *Lambeosaurus*, a contemporary crested duckbill; skull length about 32 inches. *C*, *Stegosaurus*; skull length about 16 inches. *D*, *Triceratops*, an Upper Cretaceous horned dinosaur; skull length (including frill) about 5¾ feet. For abbreviations see Figure 96. (*A*, *B* after Lambe; *C* after Gilmore; *D* after Hatcher, Marsh, Lull.)

Duck-billed dinosaurs.—Most prominent of ornithopods in the Upper Cretaceous were the hadrosaurs or trachodonts, duck-billed forms which appear to have been almost universal in distribution and are represented in modern museums by numerous skeletons from western North America. The skull structure in these forms varied enormously, but the skeleton was similar in all types. The length of the body averaged about 30 feet; and, while in many structural features they were similar to *Camptosaurus* of the preceding period, the build was somewhat heavier. In the pelvic girdle the main body of the pubis was much shortened. The hind foot (Fig. 199, *E*) had but three toes, which terminated in hoofs rather than in claws. In the manus the fifth finger had disappeared and the first was reduced; the remaining three digits ended in small hoofs.

In several instances hadrosaur mummies have been discovered in western deposits. These appear to represent specimens which had dried and mummified before burial, so that a natural cast of the skin has been preserved. This shows that the hadrosaurs were unarmored, although the skin was covered with a mosaic of small scales. A web of skin was present between the digits of the manus, and the same condition probably held true for the feet. This indicates that the hadrosaurs were amphibious in habits, probably feeding in swampy pools or about their margins. The hind limbs and the stout tail with long neural and haemal arches were probably effective swimming organs.

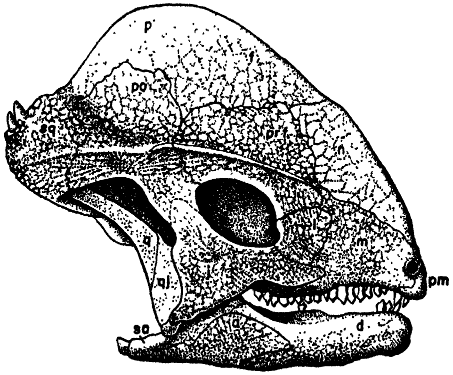


FIG. 201.—Lateral view of the skull of *Troödon*, a Cretaceous ornithopod with a greatly thickened skull roof; length about 7½ inches. For abbreviations see Figure 96. (After Brown and Schlaikjer.)

The skull in such types as *Anatosaurus* ["*Trachodon*"] and *Edmontosaurus* (Fig. 200, *A*) is readily comparable with that of a camptosaur, despite some specializations. The toothless beak was flat but greatly broadened and was presumably covered by a ducklike bill. The nostrils, usually pushed far back along the facial region, were completely surrounded by the premaxillae and nasal bones.

The teeth had remained simple leaflike structures but had multiplied enormously in numbers to form a seemingly efficient grinding apparatus for tough vegetable food. In each jaw half there was not one, but several, parallel longitudinal rows of teeth closely pressed against one another, and beneath each tooth in these series its successors were already formed and ready to function. It has been estimated that in some cases there were as many as five hundred compactly arranged teeth in a single jaw ramus, giving a total of about two thousand teeth present in the mouth of a single animal.

The appearance of numerous crested types was a peculiar feature of hadrosaur history. In some forms, such as *Kritosaurus*, a swelling—a sort of "Roman nose"—developed above the external nares, here situated well up the forehead. In *Corythosaurus* we find a thin, hollow, domelike structure capping the skull. This was shaped like a rooster's comb but was formed of bone, the premaxillae and nasals being the elements concerned. In *Lambeosaurus* (Fig. 200, *B*) this crest was present, but there was, in addition, a backwardly directed hornlike prolongation of the same bones; while in *Parasaurolophus* the crest was absent but the backward projection was a very long, tubular structure, formed entirely by the premaxillae and nasals, which thus stretched the entire length of the skull.

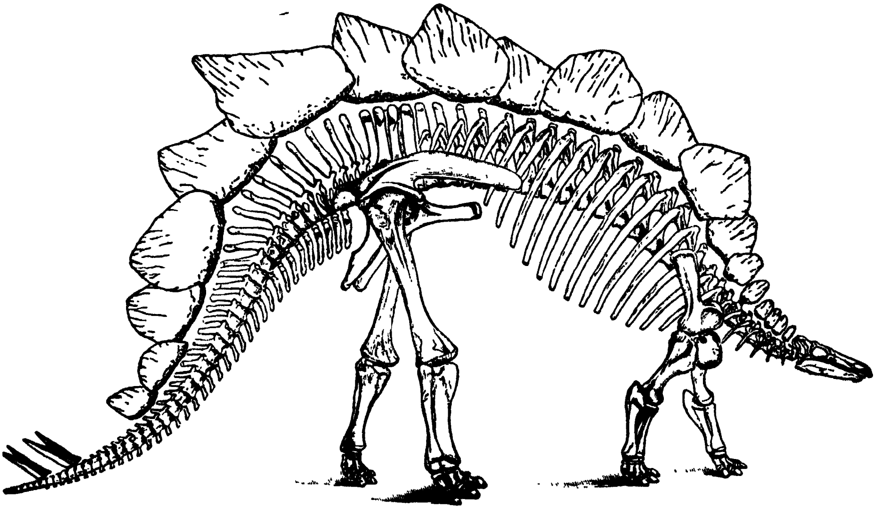


Fig. 202.—*Stegosaurus*, a Jurassic armored dinosaur about 18 feet in length. (Modified after Marsh and Gilmore.)

The details of these peculiar crests and prongs are imperfectly known, but seemingly they formed part of some unusual type of breathing apparatus; it will be noted that they were composed solely of the bones originally surrounding the nostrils. Quite possibly the crests were air-storage chambers which permitted the head of these amphibious forms to remain under water for some time while the animal was feeding; in several cases where the internal structure of the crest has been investigated, the air passage from the external nostrils follows a tortuous passage up through this area before descending to the choanae.

Hadrosaurs were exceedingly numerous in the late Cretaceous but died out completely at the end of the period. Perhaps their disappearance, like that of the sauropods, may be partly accounted for by continental elevation and the consequent drying of their marshy haunts. But not improbably a main cause for extinction may have been the contemporary gradual replacement of Mesozoic plants by modern types of vegetation to which they were not well adapted.

Stegosaurs.—Since the front legs were probably used to some extent in locomotion in most ornithopods, it would seem that reversion to a four-footed pose might readily occur. Such was the case in many ornithischian forms. But these slow-moving quadrupeds, left thus at the mercy of the carnivores, universally acquired some type of protective device in the way of armor or horns.

Earliest in appearance of quadrupedal ornithischians were members of the suborder Stegosauria, of which *Stegosaurus* (Figs. 200, *C;* 202), of the late Jurassic Morrison beds, is the most familiar. This was a fairly large dinosaur, with a length of 20 feet or more. The skull was small, the front legs short, and the back arched high over the long hind limbs. The most conspicuous peculiarity of this quadruped lay in the series of plates and spines arranged in a double alternating row down the entire length of the neck, trunk, and tail. For the most part these structures were flattened plates, which projected nearly vertically above the back. They were roughly triangular in outline, with thickened bases which were presumably tied into the skeleton by tough ligaments. The largest plates lay above the hips, the size decreasing from this point fore and aft. The tip of the tail bore two pairs of long spikes. These plates and spines would seem to have afforded protection against an attack aimed from above on the backbone and spinal cord. But there is little indication of any armor over the remainder of the body, and it would seem that *Stegosaurus* might have been easily crippled by a flank attack.

The vertebrae were still somewhat amphicoelous or, at the most, had flat-ended centra. In the pelvis (Fig. 187, *E*) the recurved ilium extended far forward; the pubis and ischum were both quite flat and broad. The hind legs were exceedingly long, giving the creature a very high hip region; the limb bones were straight with a columnar build. The front legs, on the contrary, were very short, seemingly an indication of the probably bipedal ancestry of the stegosaurs. All five digits were present in the manus, but the outer two were reduced; the pes was three-toed. The toes terminated in flattened, hoof-like structures.

The skull was very small and long but low; here, as in the sauropods, the brain was exceedingly tiny and was vastly exceeded in size by a swelling of the spinal cord in the sacral region. There was but a single row of about two dozen small teeth in each jaw half.

A somewhat smaller and more primitive relative of *Stegosaurus* was ***Kentrurosaurus*** of the late Jurassic of East Africa. In this form, plates were present only over the middle of the back and were comparatively small; spines were present not only on the tail but also over the anterior part of the body.

It is thought that this animal may still have been somewhat bipedal in habits. A still earlier relative (in fact, one of the oldest-known ornithischians of any sort) was *Scelidosaurus* of the Lias (Lower Jurassic) of England, a reptile with a length of about 13 feet. Armor plates were present, but their exact arrangement is uncertain. Probably there were two rows of oval plates with longitudinal keels, which in the shoulder region appear to have developed into longer, spiny structures. The potentiality for the development of such a type of armor was inherent, apparently, in the ancestral ornithischians; dorsal dermal plates were present even in thecodonts, and we have noted their presence in the primitive ornithopod, *Hypsilophodon*.

Ankylosaurs.—An entirely different group of armored forms, the Ankylosauria, succeeded the stegosaurs in the Cretaceous. These dinosaurs had an armor of quite a different nature and probably originated at a much later time from the primitive ornithopod stock. *Ankylosaurus*, *Palaeoscincus*, and *Nodosaurus* (Fig. 203) of the Upper Cretaceous are among the better-known members of the group. They have been termed, not inappropriately, "reptilian tanks," for, with the exception of the turtles, they were the best armored of any reptiles and show many analogies to the shelled glyptodonts of the Age of Mammals.

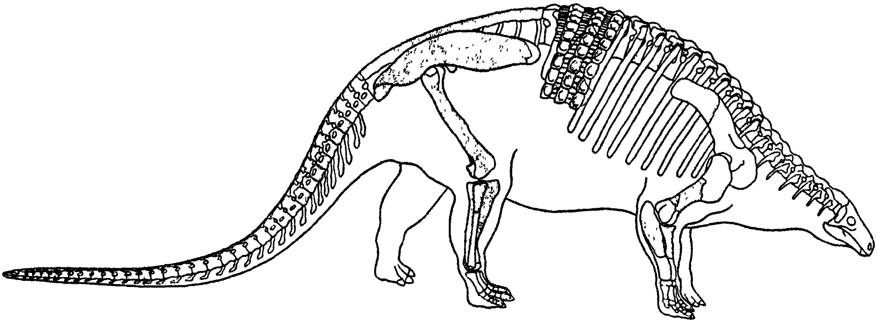


FIG. 203.—*Nodosaurus*, a Cretaceous armored dinosaur, 17½ feet in length; a few segments of the armor are indicated. (From Lull.)

The body was broad and flattened, the proportions not unlike those of a "horned toad." The entire back was covered by a tough mosaic of larger and smaller bony plates which formed a seemingly efficient carapace. The front legs, which projected somewhat at the sides, were afforded protection by long spines extending outward from the shoulder region; and the tail was incased in rings of bone and sometimes armed with long, bony spikes.

The skull was large and broad but rather short. The temporal openings had been closed over, and the flat skull roof so formed was further reinforced by an extra layer of polygonal bony plates. The dentition was weak, and the teeth were seemingly entirely absent in some cases. The limbs were short but stout. In the pelvic region (Fig. 187, *F*) the ilium flared out widely over the hip region and, reinforced by bony plates on its upper surface, effectively sheltered the thighs. The pubis had become reduced to form merely a part of the acetabulum.

In both the Lower and the Upper Cretaceous of Europe have been found somewhat smaller armored types, such as *Acanthopholis* and *Struthiosaurus*, which seem to be rather more primitive members of the same group. There have been found, in connection with them, numerous plates and spines indicating the presence of a carapace somewhat similar to that of the large forms decribed above. The skull was relatively small and primitive in nature, without the broad shape of typical nodosaurs; and temporal openings, although small, were still present.

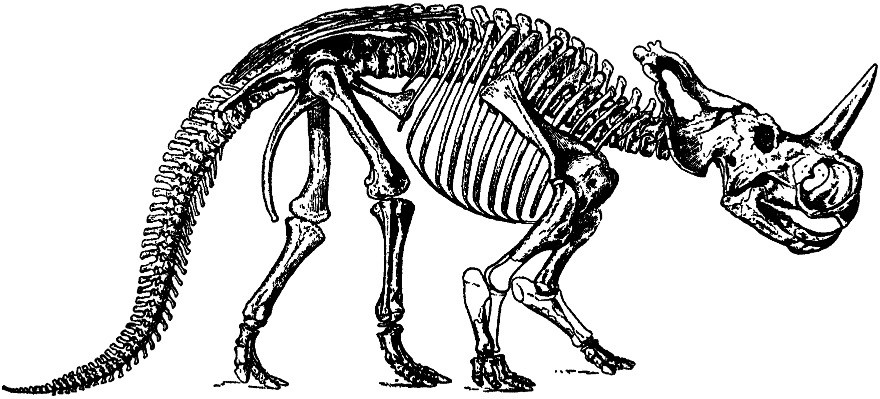


FIG. 204.—*Monoclonius*, a ceratopsian dinosaur; about 17 feet in length. (From Brown.)

Horned dinosaurs.—Last of the ornithischian groups in time of appearance were the horned dinosaurs, the suborder Ceratopsia. The entire history of this group is confined, so far as known, to the Upper Cretaceous; most forms are from North America, but the group has been identified in recent years in Asia and possibly in South America. *Triceratops* (Fig. 200, *D*) and *Monoclonius* (Fig. 204) are representative forms. These were quadrupedal dinosaurs of moderate size; *Triceratops*, for example, ranging from about 16 to 20 feet in length.

The main point of interest in these forms is the cranial structure. The head appears to be exceedingly large, making up a third or so of the total length of the body. But half of this structure is really not part of the true head region but a great frill of bone formed by extensions of the parietals and squamosals which extended back over the neck nearly to the shoulders. This frill obviously must have afforded considerable protection to the neck region, a favorite point of attack by carnivores. In some, as in *Triceratops*, this frill is a solid plate of bone; in other cases there is found a probably more primitive condition in the presence of large openings on either side.

A second curious feature of the skull lay in the development of horns. The bony horn cores are not dissimilar in appearance to those of a modern bison; and, indeed, the first-discovered specimen of ceratopsian horns was ascribed to that ruminant! In *Triceratops* there was a pair of large horns on the postorbital bones over the orbits and a median horn over the nasal region. The degree of development of these horns varied considerably. In *Monoclonius*, for example, the nasal horn is very large and the brow horns undeveloped; in another ceratopsian the reverse is true.

The remainder of the skull was much modified, in correlation with the development of these defensive structures. The temporal openings had been reduced almost to the vanishing-point. The nasal region of the skull was greatly enlarged, and the powerful beak was formed by a newly developed rostral bone comparable with the predentary in the lower jaw. Only a single row of teeth was present in the cheek region.

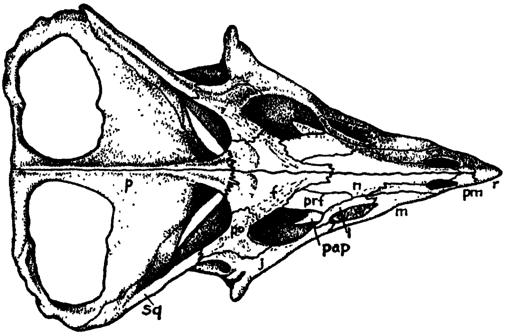


FIG. 205.—Dorsal view of skull of *Protoceratops*, a small primitive ceratopsian dinosaur from Mongolia. For abbreviations see Figure 96. (After Brown and Schlaikjer.)

The vertebrae were platycoelous. The neck was short. In the pelvis (Fig. 187, *D*) the main body of the pubis had been reduced to a short spike, although the anterior process of that bone was well developed. The hind legs were, as in all ornithischian groups, much longer than the front and terminated in four stubby, hoof-capped toes (Fig. 199, *F*) (the inner toe appears to have been reduced in some cases). All the digits were present in the manus, but the outer two were reduced (Fig. 199, *C*).

A small primitive ceratopsian is *Protoceratops* of the Upper Cretaceous of Mongolia (Fig. 205), of which there have been found numerous specimens ranging from very young individuals to adults, as well as a number of "nests" of eggs. *Protoceratops* belies its name, for horns are not present; the nasal region, however, is elevated as a potential horn-core area, and rugosities are present in some individuals in the areas in which the paired horns later developed. In contrast, the frill was well developed, although fenestrated. The structure of the frill in this form suggests that it originated primarily as a pulling-out of the back margin of the temporal region for the better accommodation of the jaw muscles and that its function as a neck protection was secondary. *Protoceratops* exhibits a very primitive feature in the presence of teeth in the premaxilla. No earlier stages in ceratopsian history are definitely known; but, as noted before, *Psittacosaurus* of the Lower Cretaceous of the same region is quite possibly an ancestral type.

Numerous as were the horned dinosaurs in the late Cretaceous, they disappeared as completely at the close of the period as did the other dinosaur groups. Except for the stegosaurs, all of the major types of dinosaurs were still in existence in the closing phases of the Mesozoic; but by the beginning of the Cenozoic all had vanished. The reign of the dinosaurs was over; the Age of Reptiles was at an end.

CHAPTER 13

BIRDS

ALTHOUGH the birds are grouped as a separate vertebrate class—Aves—they are, apart from the power of flight and features connected with it, structurally similar to reptiles. Indeed, they are so close to the archosaurians that we are tempted to include them in that group, and we may, perhaps, preferably discuss them here.

Feathers.—Birds have been called by an old writer "glorified reptiles." Feathers are in reality almost the only distinctive feature of the class, for almost every other character can be matched in some archosaurian group. Large quills form the expanse of the wing, taking rise from the back of the forearm and from the reduced fingers which form the distal part of the wing support. On the tail (which, as a bony structure, is very short) is set a spreading fan of stout feathers used as a rudder. The rest of the body is covered with a thick overlapping set of smaller, softer feathers, which forms a very efficient insulation for the control of the bird's bodily heat.

But, although the feathery covering of birds is in contrast with the horny scales which normally cover a reptile body, the difference is, in reality, not so great as it seems; for feathers are comparable to scales, with a complex structure of barbs and barbules instead of the simple scale shape.

Flight adaptations.—Unlike ordinary reptiles, birds are warm blooded; maintenance of a high body temperature is a necessity, for flight requires a great energy output over a long period. Also connected with this necessity, which demands a large oxygen supply and an efficient circulatory system, is the fact that the heart is divided completely into four chambers; those receiving fresh blood from the lungs and leading it to the body are completely separated from those taking used blood from the body to the lungs. This is a condition also found in mammals, but in birds the great arch of the aorta, which carries the blood from the heart to the body, passes over and down the right side of the chest, rather than the left, as in ourselves.

The nesting habit, contrasting with the usual lack of care of reptilian eggs, seems also to have been developed in connection with flight. The eggs must be kept warm for the maintenance of body temperature in the embryo. Further, while a young reptile makes its own way in the world from birth, the necessity of protection of the young until they have mastered the complicated business of flight seems to have rendered essential the care and feeding of the fledglings in the nest. Brain and sense organs are much modified in relation to flight. Birds depend for their main contact with the world upon sight rather than smell (in contrast to reptiles and most mammals). The eyes are large, and sclerotic plates are commonly developed in the eyeball. The bird brain is vastly enlarged compared with that of a reptile; but this enlargement appears to result not so much in an increase in intelligence as in the development of centers having to do with sight, balance, and the delicate muscular co-ordinations necessary for flight.

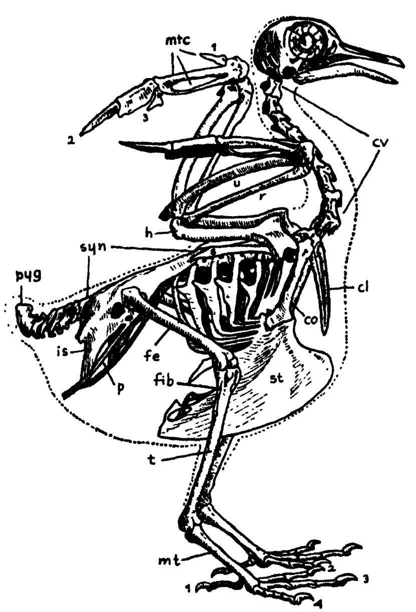


FIG. 206.—The skeleton of a modern bird. Abbreviations: *cl*, clavicle; *co*, coracoid; *cv*, cervical vertebrae; *fe*, femur; *fib*, fibula; *h*, humerus; *il*, ilium; *is*, ischium; *mt*, metatarsus (including distal tarsals); *mtc*, metacarpals; *p*, pubis; *pyg*, pygostyle; *r*, radius; *s*, scapula; *st*, sternum; *syn*, synsacrum; *t*, tibia; *u*, ulna. Digits of manus and pes numbered. (Modified from Gerhard Heilmann, *The Origin of Birds* [copyright, New York: D. Appleton & Co.], used by permission.)

Skeleton.—In the skeleton (Fig. 206) there are many modifications connected with flight. With the result of lessening the specific gravity, not only are there air sacs within the body connected with the lungs, but many of the skeletal elements, including portions of the skull and neck vertebrae, the humerus and femur, may be hollow, air-filled bones.

Wings.—The anterior limb as the actual support of the flying organs has been much modified. There is, on either side, a long, slim, backward-slanting scapula and a single coracoid attached to the edge of the sternum. There are slim clavicles which usually fuse in the mid-line to form the wishbone. The sternum is a large plate, usually with a great keel in the middle in flying birds; and to it are attached the powerful chest muscles which exert the main propulsive pull on the humerus during flight (these muscles form the white meat of the chicken).

The humerus is short and stout in most modern flying birds, with a heavy process near the head for the attachment of the chest muscles. Both bones of the lower arm are well developed and rather long; but the ulna, which carries important wing feathers at its back, is the stronger. There are four carpals, the two distal ones fused with the metacarpals. We find a reduction in the hand rather similar to that in dinosaurs, for only the three inner fingers are represented; the fourth and fifth have vanished completely. Even the three remaining are not complete. The pollex is short and usually has but one phalanx. The three metacarpals are fused with one another; the second finger usually has two free phalanges, the third but one. Almost never do these fingers bear claws; they are buried in the flesh and function only as supports for the feathers.

Backbone.—As was presumably the case with its archosaurian ancestors, the modern bird walks in a semierect position. The free vertebrae usually have a complicated but easily movable saddle-shaped set of centrum articulations in addition to the zygapophyses. The neck includes a rather variable number of elongate and freely movable vertebrae. The dorsal region, however, is very short, with only about six to ten vertebrae; and of these, several in front are often fused, as in some pterosaurs, with the effect of giving a stronger support to the muscles running to the wings. A number of posterior dorsals and the proximal caudals, as well, are joined to the original sacral vertebrae to make up an elongate synsacrum. The tail is short; following a half-dozen small free vertebrae, the few remaining ones are fused in modern flying birds into the pygostyle, which forms a support for the spreading tail feathers.

Legs.—The hind legs are reminiscent of the dinosaurs in their structure. The ilium is very much elongated and firmly bound to the synsacrum. As in dinosaurs, the acetabulum is perforated. The pubis passes down and backward, as in the ornithischian dinosaurs; there is, however, no forward branch, although this may be represented by a small process. The slim ischium passes down and back, parallel to the pubis. There is usually no ventral union of the bones of the two sides, but the ischium is usually braced by an upward extension, which meets the posterior end of the ilium, and pubis and ischium may join one another distally. The femur is short and stout, but the tibia is elongated, while the fibula is always reduced and attached to the tibia and may disappear except for its proximal end. As in the dinosaurs, the main joint with the foot lies in the middle of the tarsus; the proximal elements are fused with the tibia, the distal ones with the metatarsal elements. The foot, too, is essentially like that of many dinosaurs. The three middle toes are generally well developed; the fifth has gone without leaving a trace; and the first, often reduced or absent, has only an incomplete metatarsal and usually is turned to the rear, where it may aid in clutching a perch. The three principal metatarsals are firmly fused into a single element with separate distal ends for the toes. As in dinosaurs, the digits, with few exceptions, have the original count of 3, 4, and 5 phalanges, although the central toe is commonly the longest.

Skull.—The distinctly unreptilian appearance of the bird skull (Fig. 207) is due principally to the large orbits and large braincase; its structure is one easily derivable from the archosaurian type. Most of the sutures between bones become obliterated early in life, making the identification of elements difficult. The condyle, as in reptiles, is single; and there is no pineal opening. The orbits are very large and generally incompletely surrounded by bone. In front of the orbits (again as in dinosaurs) is an antorbital opening; postfrontal and postorbital are lacking. Behind the orbit is a single temporal opening, which, however, is presumably the two diapsid openings fused into one by loss of the bar separating them. Because of the incomplete nature of the circumorbital ring, the temporal opening usually communicates freely with the orbit. The jugal and quadratojugal pass forward as a slim bar from the quadrate; this last element is freely movable on the skull, having loose joints with squamosal, pterygoid, and quadratojugal.

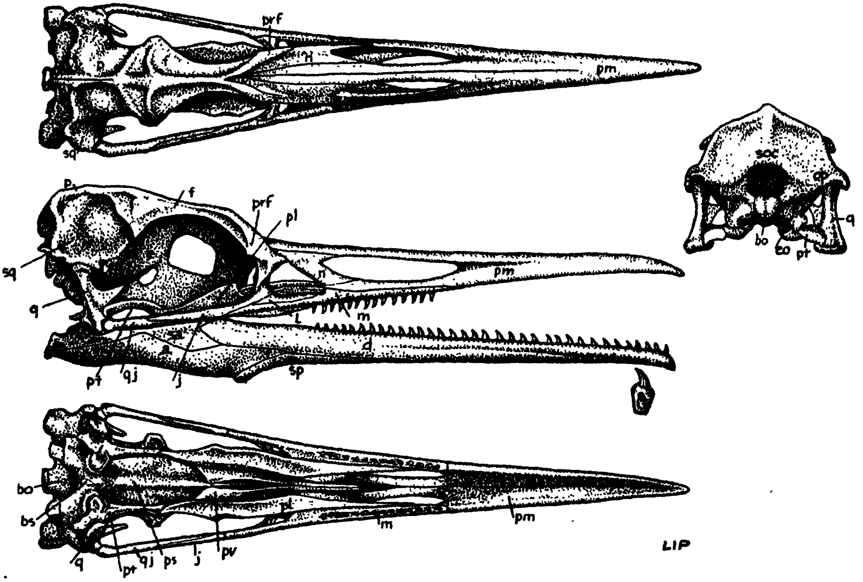


FIG. 207.—Restoration of the skull of the Cretaceous toothed bird *Hesperornis*, dorsal, lateral, ventral, and occipital views; length of original about 10 inches. For abbreviations see Figure 96. (After Heilmann, *The Origin of Birds* [copyright, New York: D. Appleton & Co.], used by permission.)

The palatal structure (Figs. 207, 208) is easily derivable from the archosaurian type. There is never any secondary palate, but the internal nares (and the external ones as well) are usually well back in the skull. Vomers, palatines, and parasphenoid are present; but there are no ectopterygoids. In the higher birds the vomers are small, the pterygoids short; the palatines extend back to a suture with the base of the braincase and have movable articulations with the pterygoids. This type of palate, termed neognathous, is markedly different from that of reptiles. An intermediate type, however—the palaeognathous—is found in certain presumably primitive types, such as the ostrich-like forms and in *Hesperornis*. This type is considerably closer to the reptile palate in that the vomers are much larger, the palatines do not come into contact with the braincase, and the pterygoids are longer and have an immovable union with the palatines. In the lower jaw all six typical reptilian bony elements are present; and, as in most archosaurians, there is an external opening between angular and surangular. Modern birds are, of course, toothless, and the beak is covered with a horny bill.

Jurassic birds.—Modern birds show many reptilian features; but even closer to the archosaurians were the earliest birds, known only from two skeletons of animals about the size of a crow from the Jurassic lithographic stone of Germany. The remains, which pertain to two related genera—*Archaeopteryx* and *Archaeornis* (Figs. 209, 210)—so closely resemble those of some of the smaller bipedal dinosaurs that they might well have been taken for reptiles, were it not for the impressions of feathers which surround them on the stone slabs on which they are preserved. The skull, as far as it can be seen, was already rather birdlike, with an expanded braincase; and, as in modern birds, the sutures were mostly closed. However, well-developed teeth, implanted in sockets, were present in the jaws. None of the bones was pneumatic. The backbone was quite simple in structure, for the centra had the primitive amphicoelous character, and all were free as far as the sacrum, which included only five or six vertebrae. The tail still had the long structure of the typical dinosaur; and the feathers were arranged in two rows along its sides. As would be expected, the hind legs were quite like those of archo-

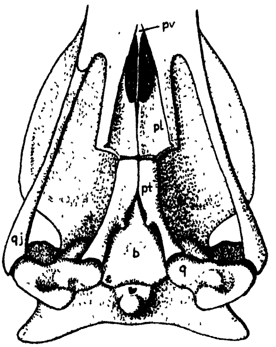


FIG. 208

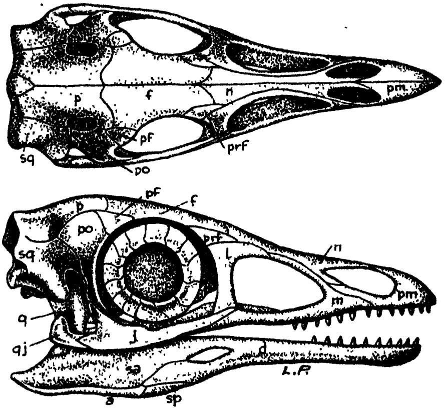


FIG. 209

FIG. 208.—The palate of a neognathous bird, based upon *Phororhacos*. Abbreviations; *b*, basicranial region; *pl*, palatine; *pt*, pterygoid; *pv*, vomers; *q*, quadrate; *qj*, quadratojugal. (Data from Andrews.)

FIG. 209.—Attempted reconstruction of the skull of the Jurassic bird *Archaeornis;* length of original about 2 inches. For abbreviations see Figure 96. (After Heilmann, *The Origin of Birds* [copyright, New York: D. Appleton & Co.], used by permission.)

saurs, for they are but little changed even in modern birds. The wings had not yet completed their transformation. The sternum was not preserved but must have been small and could not have afforded much support for pectoral muscles (incidentally, ventral ribs were still present). The front limb was still a hand rather than a wing, for the three fingers which it possessed were very similar to those of the carnivorous dinosaurs; the metacarpals were quite separate, the number of joints was complete, and each finger was clawed. It would hardly be suspected that this appendage was used for flight, had not the impression of wing feathers been found back of the ulna and manus. The flying powers, however, must have been slight, for the spread of the wing was much less than that of rather poor fliers, such as the pheasant, among modern birds. These early forms probably were forest types and did little more than plane from tree to tree or to the ground.

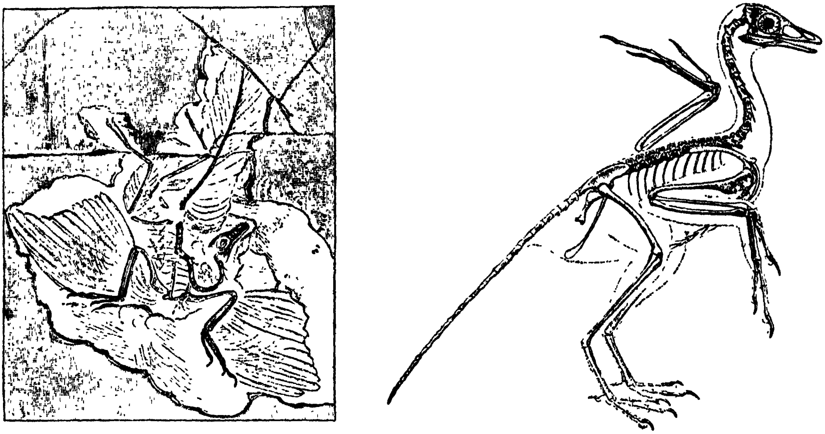


FIG. 210.—*Archaeornis*, an archaic Jurassic bird. *Left*, specimen as preserved, about ⅓ natural size *Right*, restoration. (*Left* after Evans; *right* after Heilmann, *The Origin of Birds* [copyright, New York: D. Appleton & Co.], used by permission.)

Archaeopteryx and *Archaeornis* were already definitely birds but were still very close to the archosaurian reptiles in most of their structures, and it is obvious that they were descended from that group. Their exact ancestors among the small thecodonts which include the ancestors of all the later archosaurians are unknown. The structure of the pelvis suggests that they arose from a stock close to that which gave rise to the Ornithischia. There were, however, in the limbs many features suggestive of a parallelism, if not an actual relationship, to the saurischian dinosaurs.

There has been much discussion as to the origin of flight. The most generally held theory is that the ancestral bird was a tree dweller and that flight started as a slight parachute effect as the "proavis" jumped from branch to branch, the developing wings breaking the fall on landing. A second theory is that the ancestors were ground types and that the feathered arms and tail helped increase running speed by acting as planes.

The early birds of the Jurassic were obviously sharply marked off from later types by several features which are not met with in birds of later geological times. These include the absence of pneumaticity, the primitive reptilian structure of the wing bones, and especially the long reptilian tail. They are the only known forms included in the subclass Archaeornithes.

Cretaceous toothed birds.—All other birds may be included in the subclass Neornithes, characterized by such features as a reduced tail with a fan of feathers, a well-developed sternum usually with a good keel, and the reduction and fusion of the metacarpals to the typical bird condition.

Our next glimpse of bird life is gained from the chalk beds of the Cretaceous, the only complete fossils being from the marine Niobrara formation of Kansas. This is, in a sense, unfortunate; for we know, in consequence, only sea birds and the more generalized land types are almost unknown. Two forms are known from adequate skeletons. One, *Ichthyornis* (Fig. 211), was a small form about the size of a tern, seemingly rather similar to a tern in habits and not unlike it in many structural features. In *Ichthyornis* the vertebrae were still amphicoelous, but the wings were highly developed and quite like those of later birds, and the sternum was large and keeled. Here, as in *Archaeopteryx*, teeth arranged in separate sockets were still present; and consequently we are dealing with a type intermediate between the Jurassic forms and modernized birds. A second and considerably larger bird from these deposits is *Hesperornis* (Figs. 207, 211). This remarkable form was probably much like the modern loon in habits, for it seems to have been a diving bird with powerful hind legs which spread out sidewise at the ankles to give a vigorous swimming stroke. But *Hesperonis* had already degenerated in connection with its water life, for the wings had been almost completely lost, and of the arm bones there remains only a slender humerus, while the sternum was unkeeled. This is the first of the many types of birds which have taken up a water life. As in *Ichthyornis*, teeth were present, although here they were placed in a groove rather than in sockets; and, also as in that form, there were no teeth in the premaxilla; probably the horny beak was already in process of formation.

These two birds may be gathered together in a superorder Odontognathae, in contrast with all other post-Jurassic birds; and the two known types are certainly far enough apart, judging by avian standards, to be placed in two separate orders. The incomplete glimpse which they give us of Cretaceous bird life at least shows us that the radiation of the group must have been far under way at this time to have already produced such dissimilar forms.

Tertiary birds.—All later birds may be distinguished from those already discussed by several characters: loss of teeth; the fact that the two halves of the jaw, separate until then, are fused; and a union of the posterior end of the ischium with the ilium. Such birds, we know, had come into existence by the end of the Cretaceous. A large jaw from the Upper Cretaceous of Canada (*Caenagnathus*) is suggestive of a giant bird rather than a toothless dinosaur. There are, in addition, a few other Cretaceous fragments which may be those of toothless birds; but our remains of them are very poor, and it is not until the beginning of the Tertiary that we have much information about them.

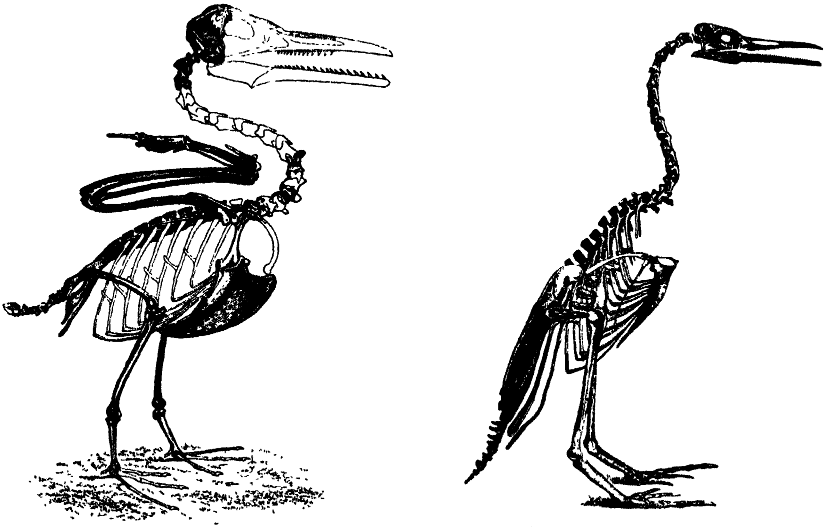


FIG. 211.—Cretaceous toothed birds. *Left, Ichthyornis*, a small form with well-developed wings, about 8 inches in height. *Right, Hesperornis*, a flightless diver, about $\frac{1}{12}$ natural size. (The feet should be directed laterally.) (From Marsh.)

And even here, it must be confessed, our knowledge is none too good. Birds are mostly small forms, and their bones and skulls are very fragile; consequently, we have but few remains, mostly of water birds. With mammals and reptiles we know more fossil forms than living ones; but among birds, as against about twenty thousand living species, we have but four or five hundred fossil forms. Even these are, for the most part, known only from a fragmentary bone or so. This leads to great difficulties in attempting to work out the paleontological history of the group, for the birds of today, despite their varied plumage, are very similar to one another in their structure. They are divided into many orders; but the differences, for example, between a humming bird and an albatross are much less than those between a seal and a cat, or between a stegosaur and a duck-billed dinosaur, forms which are commonly placed in a single order. The different orders have, in general, no more differences between them than exist between families in other classes of vertebrates, and, anatomically, generic differences are so slight that fossils are very hard to place.

Palaeognathous birds.—Of all the post-Mesozoic birds, the most interesting from the paleontological point of view are the flightless forms represented today by the ostrich, rhea, cassowary, emu, and kiwi and including a large number of interesting fossil types. These forms, here grouped together with the tinamous as a superorder, Palaeognathae, have a number of common features. Most of them, however, are associated with the fact that they have lost the power of flight; the wing skeleton in flightless forms is naturally reduced; the sternum, with weak pectoral musculature, lacks a keel, and the hind legs are powerful running organs. Since the tail is not used for flight, there is usually no pygostyle. The feathers, in correlation with the loss of flight, are usually soft and curly. But, in addition, some presumably primitive features are found in the lack of the distal fusion of pubis and ischium found in most modern birds and in the palaeognathous palatal structure described above.

Perhaps representing the central stock from which the ostrich-like birds have arisen are the tinamous (Tinamiformes) living in South America today and almost unknown as fossils. These forms have the appearance of quail or grouse but are quite different from those game birds in their structure. They are essentially ground dwellers and take to the air only in an emergency. They are exceedingly poor fliers, having little control over their flight and seldom going more than a hundred yards or so. Tail feathers are reduced or absent, but, unlike other ostrich-like birds, there is a keeled sternum.

Ratites.—From such a stock may have come the remaining, flightless members of the superorder, often grouped as ratites. Most familiar are the ostriches (order Struthioniformes), the largest of living birds. Now found only in Africa and Arabia, they are known to have existed in Eurasia in the Pliocene, while eggs of a gigantic ostrich-like bird have been found in the Pleistocene in that region. A distinguishing feature of the ostrich, in contrast to other flightless types, is the fact that there are only two toes—the third and fourth.

On the South American pampas the place of the ostrich is taken by the rhea (order Rheiformes), with a somewhat different structure (including a three-toed foot) and smaller size. Rheas are known from the Pleistocene, but farther back their history is quite unknown.

In Australia and New Guinea are the emus and cassowaries (order Casuariiformes). Among their distinguishing features is the fact that the wing is more reduced than in either of the last two orders, there being only one digit preserved, and this projecting but little from the body. These forms were present in the Pleistocene of Australia.

Still more interesting were certain fossil types present in the Pleistocene of two island regions. In Madagascar lived a number of species of "elephant-birds" (*Aepyornis*, order Aepyornithiformes), some of them as large as an ostrich, with greatly reduced wings and heavy legs. There have been found numerous eggshells, some with a capacity of two gallons. It is possible that these large birds lived until quite recent times, and their extermination may have been due to man.

New Zealand is remarkable today for flightless birds, for there are found not only the kiwi but numerous flightless rails and other ground dwellers belonging to higher bird groups. In the past there were much larger ratites, the moas (order Dinornithiformes) (Fig. 212), which ranged in size from species no larger than a turkey to creatures 10–11 feet in height. Numerous remains of these birds have been found, and even feathers have been preserved. There is proof from native camp sites that these forms were still alive when man reached the island and that they were used for food.

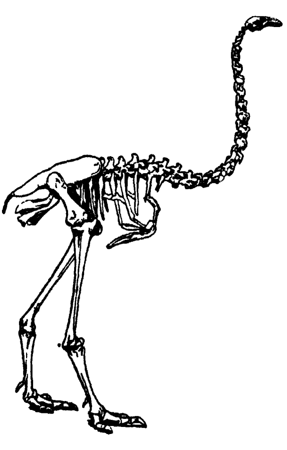


FIG. 212.—*Dinornis maximus*, one of the smaller New Zealand moas; height about 7 feet. (After Andrews.)

Quite different from the ostrich-like groups in size and general appearance are the kiwis of New Zealand (order Apterygiformes). These small birds are also practically wingless ground types with a very long bill and small eyes. They are known as fossils from the Pleistocene of New Zealand and from Australia as well.

Origin of flightless types.—It has been suggested that these various groups of flightless birds are really primitive forms that have descended from types in which flight had never been developed. But upon reflection it is obvious that such a theory is highly improbable. Even in the Cretaceous the toothed *Ichthyornis* had already developed powerful wings, and such a form as *Hesperornis* was obviously specialized rather than primitive. Further, we know that in many other higher groups of birds certain types have also lost the power of flight; the dodo, the great auk, and the flightless rail of New Zealand are all types which have reduced wings and cannot fly but yet are surely descended from flying forms.

The clue to the matter seems to be that, for many birds which seek their food on the ground, flight is necessary mainly as a protection from enemies. With freedom from carnivores, there is no reason why flight should be maintained. Almost all these flightless forms are so situated as to be practically free from enemies. There are no carnivorous mammals in New Zealand; until the arrival of man there was no ground-living enemy of any kind for the moas and kiwi. In Australia the only carnivores before the arrival of man and his dog were comparatively harmless primitive mammalian types (marsupials). The island of Madagascar is almost devoid of carnivores. The ostrich and rhea are in a worse situation, but they live in open country where carnivores cannot approach without being seen, and the speed of these forms enables them to outrun their enemies. It would thus seem that birds are likely to return to a ground life wherever conditions permit. When flight is thus abandoned, most of the common adaptations seen in these forms, such as reduction of wings and tail and development of powerful legs, would naturally follow. The resemblances between the various ostrich-like types need not, then, really indicate relationship; and below are mentioned other large birds, now extinct, which in the past evolved along similar lines.

However, certain anatomical features, such as the palate, tend to show that these forms are really related. A probable suggestion is that there existed in the early Tertiary a group of birds in which teeth had been lost but the palate had remained primitive, and which had complete wings and a keeled sternum but were comparatively poor fliers. The living tinamou may be a comparatively unchanged relict of this primitive type. In parts of the world where favorable conditions existed, these forms might have tended to stay on the ground, lose the power of flight, and develop into ostrich-like forms; in other regions they would have lost out in competition with better flying types and have disappeared.

There is little fossil evidence for such a history; but, as has been said, our knowledge of early fossil birds is very inadequate.

Neognathous birds.—All remaining birds may be grouped together as the superorder Neognathae. In these forms there is but seldom any tendency toward a flightless condition; almost always the wings and tail are well developed. As a common key character may be cited the fact that the palate is of the advanced neognathous condition described earlier.

As was noted above, the members of numerous living groups are essentially similar in internal structure, and the taxonomic position of many fragmentary fossil types is dubious. Nevertheless, it appears probable that most, if not all, of the avian orders were in existence in early Tertiary times; and some inadequately known Cretaceous types may be ancestors of the modern bird groups.

Below we shall discuss briefly the generally accepted orders of birds and a few of the more interesting fossil types. Half of the orders listed are known from Eocene representatives. However, half-a-dozen groups—Colymbiformes, Procellariiformes, Cuculiformes, Micropodiformes, Trogoniformes, and Coraciiformes—are first known in the Oligocene; the Columbiformes and Psittaciformes appear only in the Miocene; the Caprimulgiformes in the Pliocene; the small group of Coliiformes are unknown as fossils.

1. *Order Gaviiformes.*—The loons (*Gavia*, called *Colymbus* by European scientists) are northern water birds of primitive aspect which are excellent swimmers and in many adaptational features recall the Cretaceous *Hesperornis*. Unlike that ancient genus, however, the loons are good fliers with well-developed wings. This and the two following orders of marine birds, although represented in the early Tertiary, are not common as fossils.

2. *Order Colymbiformes.*—The grebes are smaller, cosmopolitan water birds which are, again, good swimmers as well as fliers. The feet, however, are not webbed; each toe has, instead, a separate broad flap of skin.

3. *Order Procellariiformes.*—The albatrosses and petrels are strong-flying oceanic birds, with very long and powerful wings; the feet, with reduced halluces, are webbed, but swimming is of secondary importance; peculiar tubular nostrils are a diagnostic feature.

4. *Order Sphenisciformes.*—The penguins, although primitive in many respects, are in many others among the most highly specialized of birds. The wings are totally incapable of functioning in flight but are powerful flippers used in swimming. The wing bones are flattened and fused into a compact, powerful fin. The foot, too, is modified for swimming; it is webbed, and the metatarsal bones are but partially fused, in contrast to their intimate union in typical modern birds.

The penguins appear to have been derived from marine flying birds similar to those of the last order, which, like the diving petrels, acquired the habit, when in pursuit of food, of flying under water as well as in the air. Presumably, in the penguin group submarine swimming became more important than flying; flight adaptations were abandoned, and the wings perfected as swimming organs. The evolution of penguins appears to have taken place in the temperate zone of the Southern Hemisphere, which is also the center of distribution of the related Procellariiformes. Some penguins are found in Antarctic waters; others have even followed a cold current northward to the Galapagos, but none has crossed the tropics to colder northern regions, where the (unrelated) auks and their allies fill a somewhat similar ecologic niche. Numerous fossil penguins, some as large as a man, have been reported from mid-Tertiary deposits in Patagonia and farther south, on Seymour Island off the shores of the Antarctic continent.

5. *Order Pelicaniformes.*—Tropic birds, pelicans, gannets, cormorants, and frigate birds are characteristic members of this group. They are, again, aquatic—mainly marine—birds, fish-eaters, and with good powers of flight. Here all four toes are included in the webbed foot. Nearly every family in the order is known from the Tertiary, and one form (*Elopteryx*), represented by limb material, is from the Upper Cretaceous. If correctly assigned, this is

the oldest of known neognathous birds. An early Tertiary type (*Odontopteryx*) is of interest in that the lost teeth were functionally replaced by a saw-toothed edge to the jaw.

6. *Order Ciconiiformes.*—A large group of water-loving birds, mainly tropical, fish-eating waders, with long legs and (usually) long bills—the herons, storks, and flamingos. The flamingos have webbed feet, but the others have so far abandoned aquatic habits for the land and for tree-perching that the web is absent. Their shore-dwelling habits are perhaps responsible for the fact that the herons (Ardeidae) and storks (Ciconiidae) are common fossil types.

7. *Order Anseriformes.*—The ducks, geese, and swans and their relatives. The flat bill, short but powerful legs with webbed toes, and strong wings are characteristic features of this group, whose members are dominantly residents of northern regions. The ducks are frequently encountered in fossil faunas.

8. *Order Falconiformes.*—This group includes the diurnal birds of prey, the vultures of the Western Hemisphere (suborder Cathartae, including the condor and the "turkey buzzard"), and the suborder Falcones, which includes the various hawks, falcons, ospreys, and eagles and, in addition, the Old World vultures and buzzards and the aberrant secretary bird of Africa. The powerful beak and equally powerful claws present in most members of the order are obvious specializations for seizing and tearing the prey. These forms are quite common as fossils. A Pleistocene vulture from the California tar pits, *Teratornis*, is the largest of all known flying birds.

9. *Order Galliformes.*—This order contains, besides the common fowl, many familiar game birds and related forms, such as pheasants, partridge, grouse, quail, turkey, and peafowl. The members of this group are, for the most part, predominantly terrestrial in their habits and are capable of only short flights. An interesting member of the order is the hoactzin (*Opisthocomus*) of South America, in which claws are present on the first two digits of the nestling's wing. This adaptation, which permits the young bird to clamber about the tree, appears possibly to be a reversion to the condition found otherwise only in the oldest fossil birds. Game birds are moderately well represented among fossil avian assemblages.

10. *Order Gruiformes.*—The order includes the cranes, rails, and many presumably allied types, mainly tropical in habitat. Typical members of the group are marsh birds, waders, and, at best, heavy fliers, which resemble the herons in their long legs and neck but differ in technical details of skull construction. The rails (family Rallidae) are common as fossils. Among the less characteristic members of this rather heterogeneous order may be mentioned the ponderous bustards of the Old World and the cariamas—long-legged South American ground birds with short wings and limited powers of flight. Fossil cariamas are known as far back as the Oligocene in South America.

Included in the same order because of their possible relationship to the cariamas is a striking group of large South American fossil birds, mainly from the Miocene, of which *Phororhacos* (Fig. 213) is a representative. This was a long-legged bird the height of a man, with a powerful beaked skull as large as that of a horse; it was obviously flightless, for the wings were much reduced. The ability of these forms to survive on the ground was rendered possible by the fact that during most of the Tertiary the placental carnivores, those characteristic enemies of ground birds, were absent from South America.

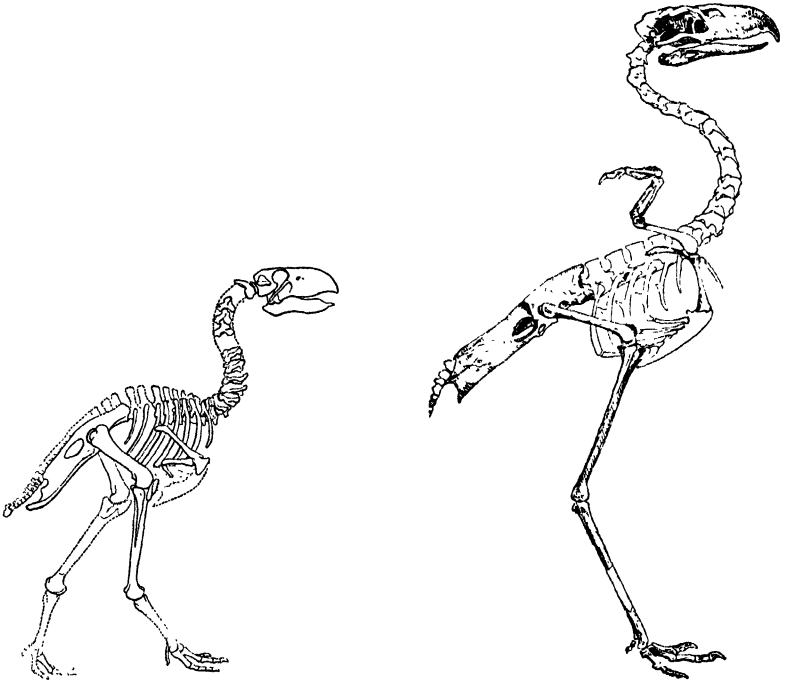


FIG. 213.—*Left*, *Diatryma*, an Eocene flightless bird, about 7 feet in height. (From Matthew and Granger.) *Right*, *Phororhacos*, a giant flightless bird from the Miocene of South America; original about 5 feet in height. (From Andrews.)

11. *Order Diatrymiformes.*—Placed here because suspected of possible relationship to the cariamas is a group of still larger, extinct flightless birds, characteristic of the early Eocene of North America and Europe. *Diatryma* (Fig. 213) was some 7 feet in height, with much-reduced wings, massive legs, and (as in the phororhacids) a large head with a powerful beak. The appearance of this great bird at a time when mammals were, for the most part, of very small size (the contemporary horse was the size of a fox terrier) suggests some interesting possibilities—which never materialized. The great

reptiles had died off, and the surface of the earth was open for conquest. As possible successors there were the mammals and the birds. The former succeeded in the conquest, but the appearance of such a form as *Diatryma* shows that the birds were, at the beginning, rivals of the mammals.

12. *Order Charadriiformes.*—This order includes such marine types as auks, gulls, and terns and numerous shore birds, such as the plovers, sandpipers, and snipe. The plovers (Charadriidae) and snipe (Scolopacidae)—shore birds with long, slender bills and long legs—are common in fossil form in the Tertiary as well as in the Pleistocene. The gulls and terns (Laridae)—long-winged, marine, flying forms—were present in the Eocene; from that epoch, too, date the auks and their relatives (Alcidae), likewise marine but stoutly built and short-winged. The great auk—a flightless, penguin-like bird which inhabited the North Atlantic—is now extinct but hardly to be considered as a fossil form.

13. *Order Columbiformes.*—The doves and pigeons. A cosmopolitan group of strong-flying, vegetable-feeding forest dwellers, little known in the Tertiary but not uncommon in the Pleistocene. An interesting series of specialized forms, of which the dodo of Mauritius is the most familiar, became large flightless types inhabiting islands in the Indian Ocean; these are now extinct.

14. *Order Psittaciformes.*—The parrots. A group of American birds, with characteristic bills and with a type of foot structure termed zygodactylous, in which two of the four toes (first and fourth) are turned backward. Now confined almost entirely to the tropics, the oldest—Miocene—parrots are known from Europe and North America.

15. *Order Cuculiformes.*—Cuckoos and road runners; apparently related to the parrots but often considered as constituting a separate order. As in the parrots, the foot is zygodactylous. Fossil forms are few.

16. *Order Strigiformes.*—The owls, nocturnal birds of prey. The adaptive features, such as a sharp beak and powerful claws, are similar to those of the day predators (Falconiformes), but more basic structural characters show the two groups to be distinct; the forward-turned eyes of the owl furnish one readily recognizable contrasting feature. Owls are known from all Tertiary epochs.

17. *Order Caprimulgiformes.*—The oilbirds and goatsuckers (including the familiar whippoorwill); peculiar nocturnal birds with a compact body and a broad, short bill bordered with stiff bristles. Poorly known in the fossil state.

18. *Order Micropodiformes.*—Swifts and hummingbirds. Small birds with rapid flight and correlated wing and breast specializations. A few fossil swifts are known, but the tiny and still more specialized hummingbirds are unreported.

19. *Order Coliiformes.*—The colies, small African birds which superficially resemble finches but are structurally quite distinct; unknown as fossils.

20. *Order Trogoniformes.*—The trogons are tropical forest birds with short, powerful bills and a peculiar foot in which the second toe is turned backward with the first. Trogons are known from the Oligocene of Europe, a time when the climatic conditions in the North were presumably more moderate than in later epochs.

21. *Order Coraciiformes.*—A rather miscellaneous assemblage including kingfishers, bee eaters, rollers, hornbills, etc., mainly tropical birds which have little in the way of obvious common features except arboreal habits and the usual possession of an elongate bill. Apart from an Oligocene European representative of the rollers, which now inhabit the Old World tropics, we know little of these forms as fossils.

22. *Order Piciformes.*—Including the woodpeckers and the toucans and various other tropical birds. The Piciformes are all stout-billed, and the woodpeckers have the peculiar zygodactylous type of foot noted above. Our knowledge of the group as fossils is almost entirely confined to the woodpeckers (Picidae), of which there are possibly Eocene and definitely Miocene representatives.

23. *Order Passeriformes.*—The perching birds, the "highest" of bird orders. A characteristic feature is the perching type of foot, with the very large first toe directed straight back and opposed to the other three, giving an effective grasp on the limb. Flight is usually highly developed, and arboreal life is general. There are a few relatively primitive tropical families; all the others are songbirds (suborder Passeres), which include almost all the smaller familiar birds. The Passeriformes comprise about half the present bird population. Fragmentary remains of perching birds are reported from the Eocene, but finds are few until the late Tertiary and Pleistocene; it is probable that the expansion of the group took place at a relatively late period. Even in the Pliocene and Pleistocene the known remains are few when considered in relation to the modern abundance of the group; however, small size and woodland habitat are features which tend to reduce the chances of adequate fossilization in this group.

Summary.—The history of birds may be summarized as follows: (1) the appearance in the Jurassic of primitive arboreal forms with feathers and a feeble type of flight but with an essentially reptilian skeleton; (2) the development by the Cretaceous of birds which still possessed teeth but in which the skeleton was essentially like that of modern birds and flight was well developed; (3) an early dispersal of birds in which teeth had been lost but in which the power of flight was comparatively poor; these are represented today only by a few ostrich-like flightless birds and the tinamous; (4) the appearance and radiation, by the beginning of the Tertiary, of more modernized orders which now make up the vast majority of the world's bird population.

CHAPTER 14

MAMMAL-LIKE REPTILES

THE relatively late time at which the mammals took over the world's supremacy from the reptilian dynasties would lead one to think that the stock from which they sprang must have been one developed at a comparatively late date in reptilian history. This, however, is exactly the reverse of the true situation. The mammal-like reptiles, constituting the subclass Synapsida, were among the earliest to appear of known reptilian groups and had passed the peak of their career before the first dinosaur appeared on the earth.

Primitive synapsids were already present in the late Pennsylvanian and took a leading role in the archaic reptilian radiation of Permian times. Although the central types were carnivores, herbivores developed as well. A majority of known Permian reptiles were members of this group; apart from the cotylosaurs, all other reptile stocks were at that time represented only by small and seemingly rare forms.

In the Triassic, however, conditions altered. The herbivorous types rapidly disappeared, and the carnivorous forms were supplanted by the developing dinosaur stock. The synapsids rapidly dwindled in numbers during the period and (except for a few rare or doubtful genera) had vanished at its close. Many millions of years were to pass before the mammalian descendants of the synapsid group were to rise to a position of dominance.

Since the various synapsid types cover the entire range of the vast structural gap existing between the ancestral reptiles and forms extremely mammal-like, it is hardly to be expected that there would be many diagnostic features common to all members of the subclass. The central stock of the group, as has been said, consisted of carnivorous types. There was in the dentition a tendency toward a differentiation of the tooth row, the development of varied types of teeth to subserve various functions—a tendency which reached its climax in the mammals. Synapsids progressively improved the primitive clumsy limb structure found in the stem reptiles. Here, however, the trend was solely toward improvement in quadrupedal locomotion; there were (in contrast to the archosaurs) no bipedal tendencies.

The one diagnostic feature common to all members of the group was the presence of a single lateral opening in the temporal region—a condition found in no other major reptilian stock. This fenestra was primitively situated on the lateral, rather than the upper, surface of the skull and was of small size, with the postorbital and squamosal joining above it; it became enlarged, however, and extended upward to reach the parietal in more advanced forms. The pineal opening persisted in almost every synapsid. The eardrum lay, as in reptiles generally, at the back margin of the skull just above the jaw joint, but there is seldom any notch or excavation of the skull connected with it. There was comparatively little loss of cranial elements; but the postparietals (usually fused into a single bone) were, with the tabulars, pushed down onto the back of the skull, and in advanced forms the elements surrounding the orbits were reduced in number. The vertebrae were primitively amphicoelous, and double-headed ribs were present the length of the trunk. A diagnostic feature is the presence of two coracoid elements in the shoulder (Fig. 222), a new posterior one in addition to the anterior element which is present alone in most other reptiles. The dermal shoulder girdle was always retained and usually included a cleithrum in the older types.

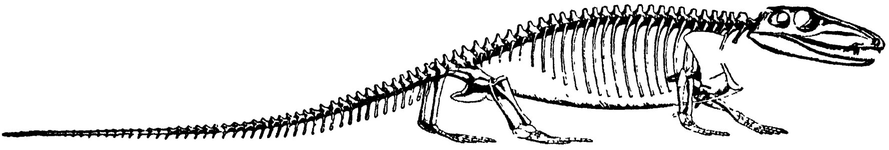


FIG. 214.—*Varanosaurus*, a primitive pelycosaur; length of original about 5 feet

The whole series should, perhaps, be divided into a considerable number of groups of equal rank. But it so happens that the primitive Lower Permian forms are found abundantly only in the Texas red beds of North America (more rarely in Europe), while the later Permian and Triassic types are found mainly in the South African Karroo series. This cleavage of the group may be used as a basis for a somewhat illogical but fairly convenient division into two orders—the Pelycosauria (or Theromorpha), primitive forms; and Therapsida, the advanced South African types. To this we shall add, as an appendix, a third order—Ictidosauria—for the reception of a few late, rare, and advanced forms which appear to lie close to the mammalian boundary.

Pelycosaurs.—The primitive synapsids are among the commonest animals found in the red beds of Texas, dating from late Carboniferous and early Permian times. Scattered remains are found in beds of like age in other areas of North America and western Europe; representatives from other times or regions are rare and of doubtful nature. A primitive member of the order was *Varanosaurus* (Fig. 214), a small form not more than 3 feet in length even with the inclusion of a very long tail. The proportions of this form were not unlike those of many lizards. In internal structure there were many similarities to the cotylosaurs from which these types had arisen. The limbs, while rather longer and slimmer than those of cotylosaurs, still resembled them in most features. The neural arches of pelycosaurs (Fig. 215) were (as in most reptiles) narrower than those of the cotylosaurs, and the neural spines somewhat taller; in *Varanosaurus*, however, the arches are still somewhat swollen—presumably a primitive feature. Intercentra were still present throughout the column, and the old scales were still present on the ventral side as abdominal ribs in most pelycosaurs. The snout was rather long; the skull rather taller and narrower than in the cotylosaur types. The teeth along the jaw margins were numerous and mostly of rather uniform size in *Varanosaurus* and its close allies; a pair of teeth lying near the front end of each maxilla may, however, be considerably longer; they appear to represent the first stage in the development of the canine teeth characteristic of mammals. *Varanosaurus* was not improbably a fish-eating reptile which spent much of its time in the water—habits which here may be truly primitive in character and reminiscent of the amphibian forebears of the group. The related genus *Ophiacodon* was a much larger animal, one species of which may have been nearly a dozen feet in length.

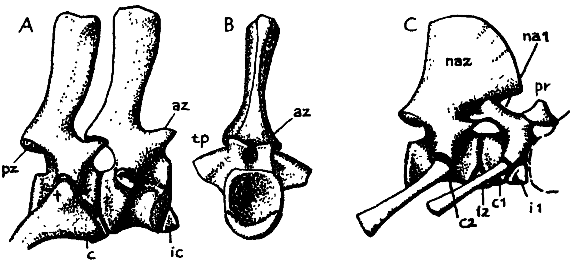


FIG. 215.—Vertebrae of a primitive pelycosaur, *Ophiacodon*. *A*, *B*, Posterior cervical vertebrae, lateral and anterior views. Abbreviations: *az*, anterior zygapophysis; *c*, capitulum of rib; *ic*, intercentrum; *pz*, posterior zygapophysis; *t*, tubercle of rib; *tp*, transverse process. *C*, Atlas and axis, condyle of skull in dashed line; *c1*, *c2*, centra of atlas and axis; *i1*, *i2*, intercentra of the same; *na1*, *na2*, neural arches; *pr*, proatlas, a neural arch whose centrum is presumably fused into the basioccipital. (After Case and Williston.)

A second and very different group of pelycosaurs is that represented by *Edaphosaurus* (Figs. 216, 217) and *Casea* (Fig. 218). These animals were apparently herbivores. The postcranial skeleton was, on the whole, rather similar to that of *Varanosaurus* but with a somewhat clumsier build and a broad, barrel-shaped trunk, presumably for the reception of masses of soft vegetation. *Edaphosaurus* presents an unusual feature because of the presence of greatly elongated neural spines rising high above the back and studded with small cross-bars, giving somewhat the effect of a full-rigged ship. It seems certain that in life the spines were connected by membranes, forming the whole into a "sail." Similar structures were formed independently in other pelycosaur genera. The function of this sail—if any—is quite uncertain. As good a guess as any is the suggestion that it was a heat-radiating device which may have aided in control of internal temperature.

The skull was short and very different from that of *Varanosaurus*. The teeth were rather blunt, and there is no trace of canine differentiation; *Edaphosaurus* has, in addition, highly developed upper and lower masticatory plates, studded with teeth, lying within the mouth.

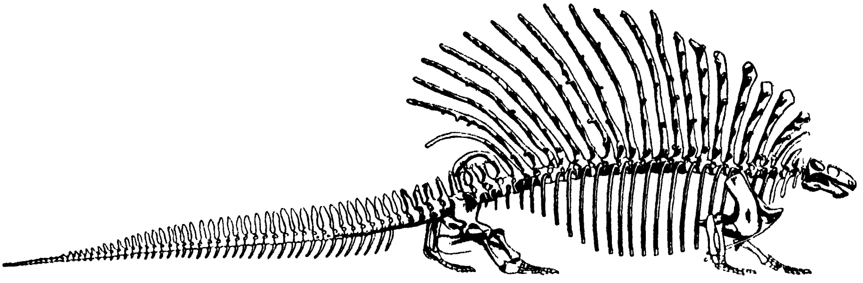


FIG. 216.—*Edaphosaurus* (*Naosaurus*), a long-spined, herbivorous pelycosaur; maximum length about 11 feet.

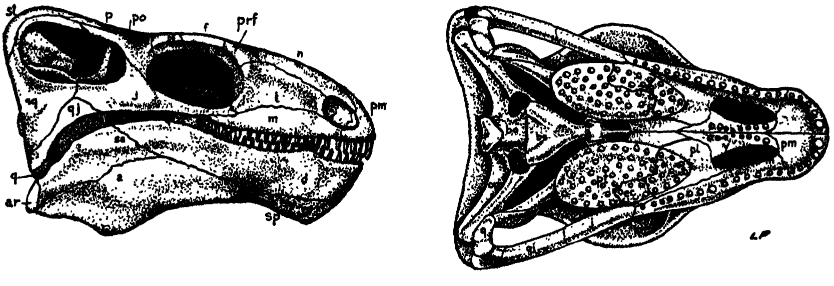


FIG. 217.—The skull of *Edaphosaurus*; length of specimen about 6 inches. For abbreviations see Figure 96.

Despite its specializations, *Edaphosaurus* was an ancient type, for characteristic spine fragments are recorded from the late Carboniferous. The earliest species were of small size; the largest Permian specimens, on the other hand, had a length of about 11 feet. *Casea* was a small pelycosaur, but a large relative—*Cotylorhynchus*—is estimated to have weighed about a third of a ton.

A third and final major group of pelycosaurs is that which includes *Dimetrodon* (Figs. 219; 220; 230, *A*), an aggressive carnivore which is the commonest of reptiles in the Lower Permian of North America. *Dimetrodon* is specialized in the presence of a great "sail" comparable to that of *Edapho-*

saurus but lacking the cross-bars. There were, however, other members of this group in which the sail was not developed, and the dimetrodonts are of interest as a stock from which the therapsids (and eventually the mammals) appear to have been derived.

The postcranial skeleton is generally comparable to that of other pelycosaurs; but the body was rather slim, and the limbs, although old-fashioned in construction, are somewhat more slender than in most early Permian reptiles, and suggestive of a relatively rapid gait. The skull was high and narrow, the face rather long; posteriorly the skull margins curved downward and even forward toward the jaw articulation—a feature repeated in many therapsids. The jaws were armed with compressed, sharp-edged teeth, well differentiated—particularly in the upper jaw—for predaceous habits. In the premaxilla were a limited number of teeth for biting and grasping, which are comparable to the incisors of therapsids and mammals. Separated from them by a "step" which may contain a few small teeth, we find on the maxilla a pair of large teeth, alternately replaced, which correspond to the canines of higher types, and behind these a series of smaller cheek teeth. The lower teeth are differentiated also, but to a lesser degree. The angular bone near the back of the jaw bears a curious flange of unknown function, separated by a notch from the main portion of the mandible. This feature is repeated in therapsids and is one of the many diagnostic characters which indicate that

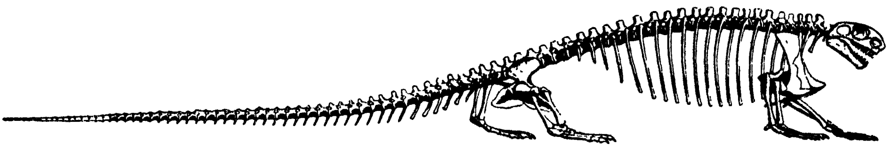


FIG. 218.—*Casea*, a short-spined herbivorous pelycosaur related to *Edaphosaurus;* length about 4 feet.

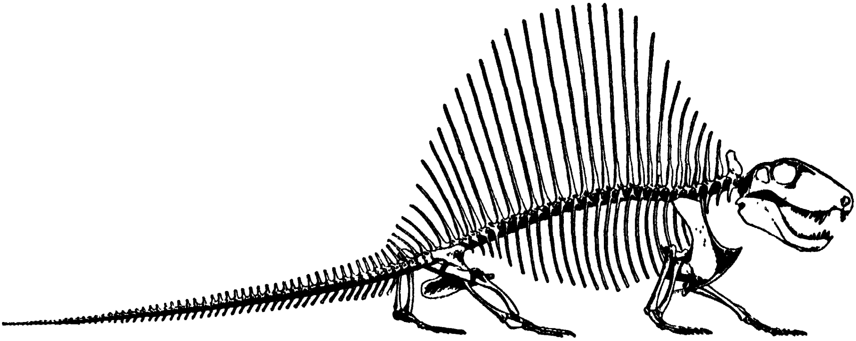


FIG. 219.—*Dimetrodon*, a long-spined predaceous pelycosaur; maximum length about 11 feet

the *Dimetrodon* group (although not this genus) gave rise to the therapsids which in the later Permian and early Triassic succeeded the pelycosaurs as the dominant land vertebrates of their times.

The forms customarily placed in the Pelycosauria are confined to the late Pennsylvanian and Lower Permian. There are, however, a few synapsids in the later Permian of South Africa and Russia which are more primitive than their therapsid contemporaries and may be surviving pelycosaurs. Problematical is a series of small South African types such as *Galepus* (Fig. 221), usually termed dromasaurs. The skull and skeleton are comparable with those of pelycosaurs, particularly some of the edaphosaur group; the one certain advanced feature is the loss of phalanges in the toes, so that the advanced mammalian count of 2–3–3–3–3 is present.

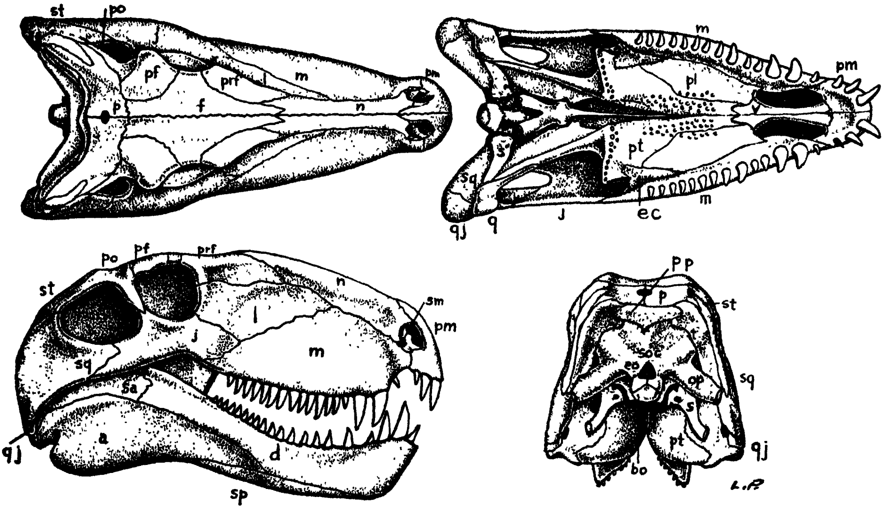


FIG. 220.—The skull of *Dimetrodon*. *Above*, dorsal and palatal views; *below*, lateral and occipital views. For abbreviations see Figure 96.

Therapsids.—As members of the order Therapsida may be grouped the numerous mammal-like types which, best known from the richly fossiliferous Karroo beds of South Africa, flourished from Middle Permian to Lower and Middle Triassic times. To this group belong all the carnivorous reptiles of the later Permian, as well as a host of herbivorous forms. So varied are these types that they are often considered to constitute a number of distinct (although closely related) orders.

Because of the wide radiation of the group, absolute diagnostic characters are rare. The evolutionary trend of the main line of therapsid development may be illustrated by a consideration of the structure of one of the later and more progressive forms.

Structure of Cynognathus.—*Cynognathus* (Figs. 228–30) was a Lower Triassic therapsid which we shall note later to be a member of the very mammal-like cynodonts. This reptile was a rather lightly built and seemingly active four-footed carnivore, with a maximum length of 4 or 5 feet.

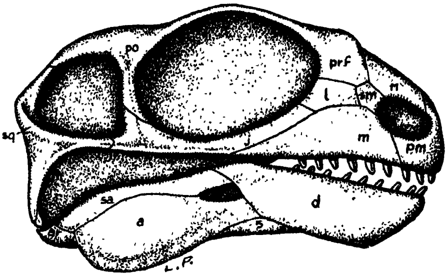


FIG. 221.—*Galepus*, a primitive synapsid from the South African Permian; length about 1½ inches; *s*, splenial. For other abbreviations see Fig. 96. (After Broom.)

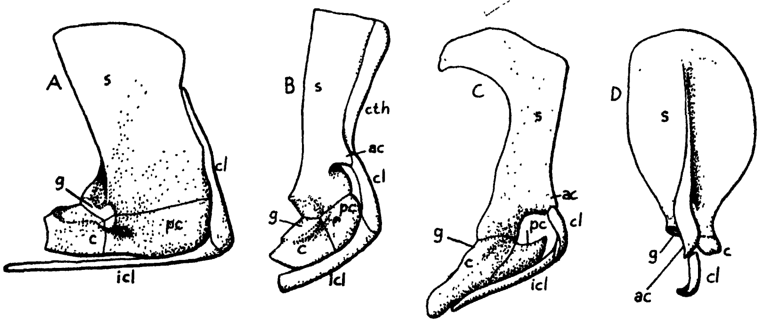


FIG. 222.—Shoulder girdles of synapsids and mammals: *A*, the pelycosaur *Ophiacodon; B*, the therapsid *Kannemeyeria. C*, the monotreme *Ornithorhynchus; D*, the marsupial *Didelphys;* Abbreviations: *ac*, acromion; *c*, coracoid; *cl*, clavicle; *cth*, cleithrum; *g*, glenoid cavity; *icl*, interclavicle; *pc*, procoracoid; *s*, scapula. (*A* after Williston; *B* after Pearson.)

In the skull the pineal opening is small but still present. Many therapsids have a small median bony element—the preparietal—associated with it; this is, however, absent in *Cynognathus*. The temporal opening is much expanded and reaches up to the parietal; the postorbital and squamosal no longer meet each other above this fenestra (but have gained a secondary contact below it). The circumorbital series of bones has dwindled; the prefrontal and lacrimal are small; and the postfrontal has disappeared. The quadratojugal is small and closely attached to the equally reduced quadrate, and these two bones are rather loosely connected with the rest of the skull. On the under side of the skull the most obvious development is the presence of a secondary palate. The two vomers have fused into a single bar which sends up a process in the mid-line. Extensions from the premaxillae, maxillae, and palatines have formed a flat plate extending across below the old level of the roof of the mouth, so that a hard secondary palate is formed with the internal opening of the nostrils passing backward through the space above it.

There are no longer any interpterygoid vacuities, for the two pterygoids have fused with each other and the narrow base of the braincase to form a solid, longitudinal bar. The pterygoids have shortened and no longer extend back to the quadrates, although the epipterygoids above them may reach this far back.

The condyle has divided into a double structure, in contrast with the primitive single condition. The occipital surface of the skull is a nearly solid plate made up of the combined occipital bones and the opisthotics, together with the postparietal and the tabulars above. In addition to the ordinary bones of the braincase, the epipterygoid forms a flat plate applied to the side of the braincase in front of the proötic; and in the more anterior portion there appears to be an ossification corresponding to the sphenethmoid of amphibians and reptiles and the presumably homologous presphenoid of mammals. The stapes extends as a slim rod from the inner-ear opening to the quadrate.

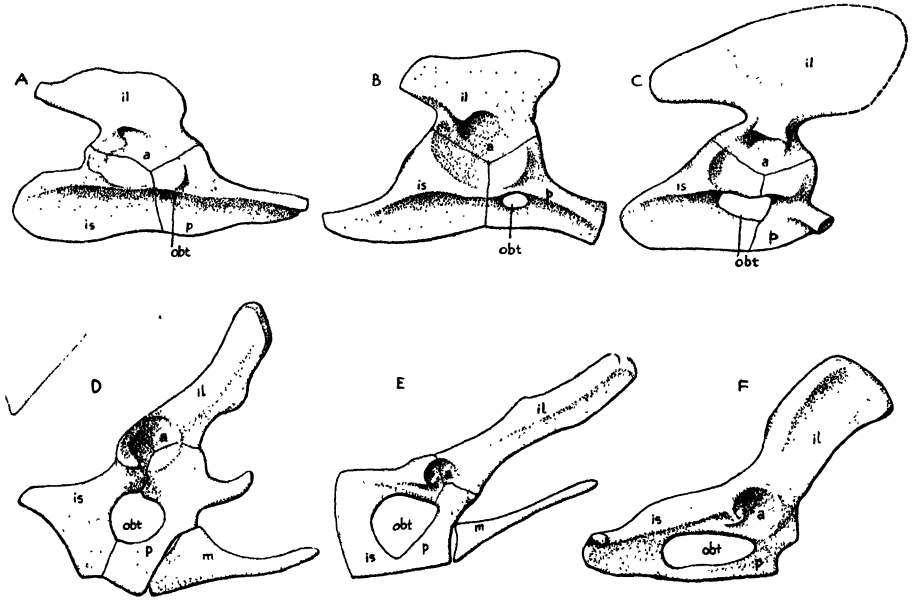


FIG. 223.—Pelvis of synapsids and mammals: *A*, the pelycosaur *Dimetrodon; B*, the gorgonopsian *Lycaenops; C*, the cynodont *Cynognathus; D*, the monotreme mammal *Ornithorhynchus; E*, the marsupial *Didelphis; F*, the Miocene canid *Daphoenodon*. Abbreviations: *a*, acetabulum; *il*, ilium; *is*, ischium; *m*, marsupial bone; *obt*, obturator foramen—enlarging to form a fenestra in therapsids and mammals; *p*, pubis. (*B* after Broom; *C* after Gregory and Camp; *F* after Peterson.)

All the bones of the primitive reptilian lower jaw are present (except that there is but one coronoid) (Fig. 230, *C*), but the dentary is greatly enlarged at the expense of the other elements, sending backward and upward a large process which nearly touches the squamosal.

The dentition is differentiated into a small number of nipping teeth, comparable with the human incisors, in the premaxilla and front of the dentary; a large "canine" tusk lying behind a step in the maxilla; and a series of cheek teeth, most of them with several cusps. Teeth are absent from the palate and the inner surface of the lower jaw.

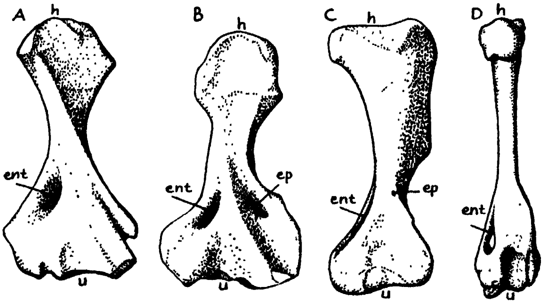


FIG. 224.—The humerus of synapsids and mammals; dorsal views: *A*, the pelycosaur *Dimetrodon* *B*, the pelycosaur *Edaphosaurus; C*, a cynodont (*? Diademodon*); *D*, the Oligocene canid *Daphoenus*. Abbreviations: *ent*, entepicondylar foramen; *ep*, ectepicondylar foramen; *h*, head; *u*, articular surface for the ulna. (*C* after Watson; *D* after Hatcher.)

Intercentra have disappeared from the backbone, although the centra are still amphicoelous. There are still freely movable, double-headed ribs all the way from the neck to the base of the tail.

The limbs in advanced therapsids are greatly changed from the primitive sprawling position. The elbow has been moved back and the knee forward, so that the legs tend to be more underneath the body, making support easier. Associated with this are many changes in the musculature and in the shape of many of the bones. The shoulder girdle (Fig. 222, *B*) still consists of a dermal girdle, including a stemmed interclavicle and clavicles (the cleithrum has disappeared) and a primary girdle of scapula and two coracoid elements. The front edge of the scapula is turned out (the beginning of the mammalian spine) with the clavicle attaching to the projecting spine at the lower end of the ridge. In the pelvis (Fig. 223, *C*) the ilium extends forward rather than back, as primitively, in relation to a changed position of the muscles, and is attached to an increased number of sacral ribs. The pubis and ischium have

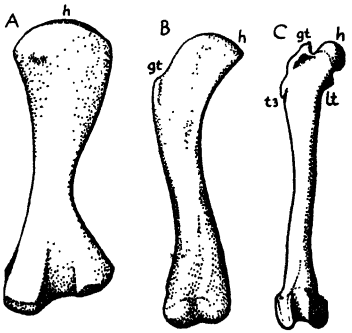


FIG. 225.—The femur in mammal-like reptiles and mammals: *A*, the pelycosaur *Ophiacodon; B*, a cynodont; *C*, the Oligocene canid *Daphoenus*. Abbreviations: *gt*, greater trochanter; *h*, head of femur; *lt*, lesser trochanter; *t3*, third trochanter. (*A* after Case and Williston; *B* after Watson; *C* after Hatcher.

shifted toward the back (also in correlation with muscular changes), and a circular opening has appeared between and partially separating them. The femur (Fig. 225, *B*) has developed a head at the side rather than the end of the bone in relation to its forwardly rotated position, and on the outer side there is a large trochanter for muscles which come from the ilium and aid in its backward push. The toes are all, except the first, of nearly equal length, in correlation with the more directly fore-and-aft motion of the limbs; and each has but three functional segments. But while this foreshadows the mammalian condition, the old reptilian phalangeal formula of 2–3–4–5–3 still persists in *Cynognathus* and related types, for vestiges of the superfluous phalanges are still present in the third and fourth toes (Figs. 226, *B*; 227, *B*).

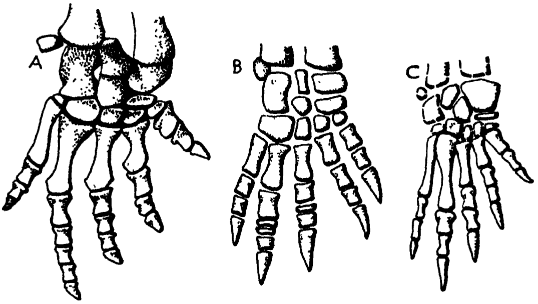


FIG. 226.—The manus in mammal-like reptiles: *A*, the pelycosaur *Ophiacodon*; *B*, the gorgonopsian *Lycaenops*; *C*, the advanced therocephalian *Ericiolacerta*. (*A* after Case and Williston; *B* after Broom; *C* after Watson.)

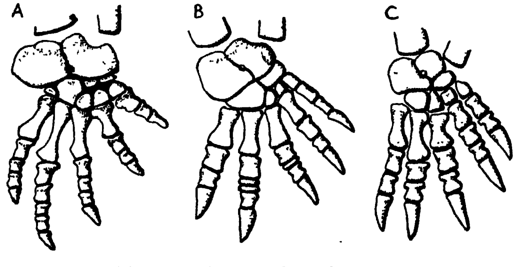


FIG. 227.—The pes in mammal-like reptiles: *A*, the pelycosaur *Ophiacodon*; *B*, the gorgonopsian *Lycaenops*; *C*, the therocephalian *Whaitsia*. (*A* after Case and Williston; *B*, *C* after Broom.)

The skeleton of such a reptile approaches in many features that of the mammals. It would be of interest to know whether these forms resembled mammals as much in other features; but we know almost nothing of other organ systems, except that the brain was still small and apparently reptilian in organization. The warm-blooded condition of mammals is seemingly correlated with their active mode of life. Activity seems to have been a keynote in the development of these carnivorous therapsids, and it is not impossible that this physiological change had already begun in them. A cold-blooded reptile may cease breathing for a time without harm, but not a mammal. The secondary palate of mammals seems to be an adaptation preventing interference with breathing during mastication; the presence of this structure in ad-

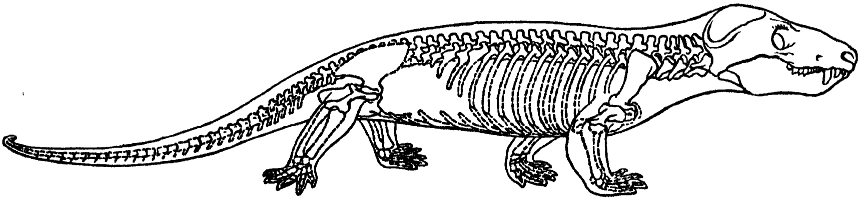


FIG. 228.—The skeleton of the Lower Triassic cynodont *Cynognathus*, about $\frac{1}{18}$ natural size. (From Gregory and Camp.)

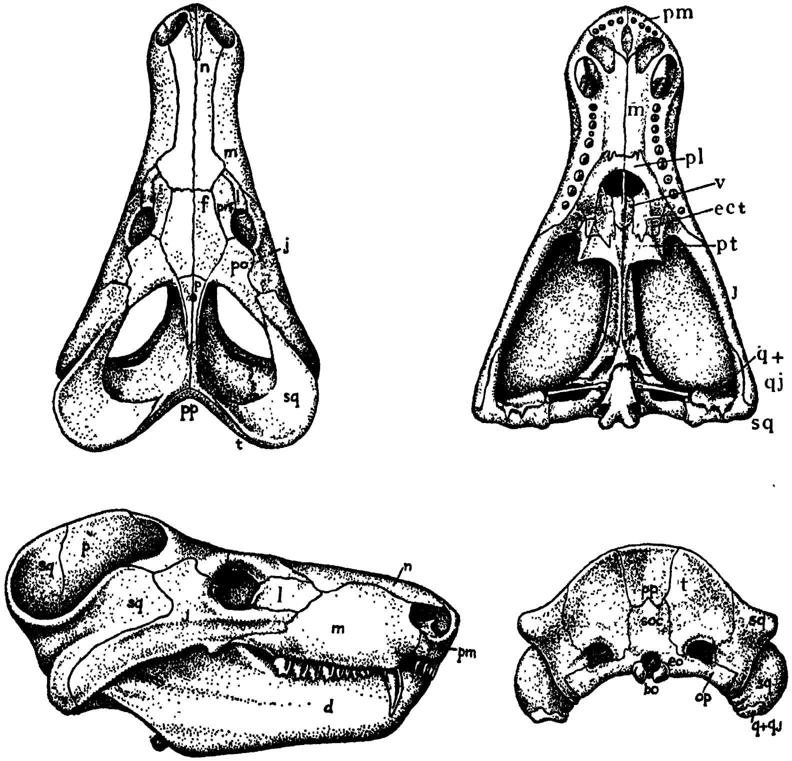


FIG. 229.—The skull of the cynodont *Cynognathus;* length of original about 18 inches. For abbreviations see Figure 96. (After Seeley, Broom, and Broili and Schroeder.)

vanced therapsids is suggestive. Whether hair was already beginning to replace scales is, of course, unknown. Nor have we any knowledge of reproductive processes; but, since the most primitive living mammals are still egg-laying types, this was presumably also the case in *Cynognathus*. The nursing habit seems to have been earlier in appearance, but whether early enough to have been present in advanced therapsids cannot be guessed.

Dinocephalians.—The oldest and, in most respects, the most primitive of therapsid suborders is that of the "giant heads"—the Dinocephalia—which flourished in the Middle Permian of South Africa and Russia. The name refers to a peculiar domelike thickening of the skull roof. The skull, except for this peculiarity, was quite primitive and resembled that of the *Dimetrodon*-like pelycosaurs in many features, such as the single condyle, lack of a secondary palate, the primitive paired vomers, and a fairly small dentary. However, a number of therapsid changes had occurred, such as the fusion of the pterygoids with the base of the braincase and reduction of the quadratojugal. Partly in correlation with the large size of these animals, the limbs are massively constructed, although turned well in toward the body in therapsid fashion. The girdles were still quite primitive. On the other hand, the phalangeal formula appears already to have been reduced to the mammalian count.

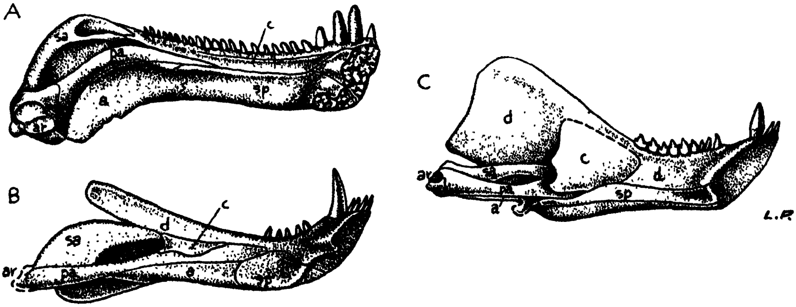


FIG. 230.—Jaws of synapsids, from the inner side. *A*, The pelycosaur *Dimetrodon; B*, the gorgonopisan *Cynarioides; C*, the cynodont *Cynognathus*. For abbreviations see Figure 96. (*A* after Williston; *B* after Broom; *C* after Broom and Watson.)

Two main types of dinocephalians are known. One, typified by *Titanosuchus* and *Jonkeria* (Figs. 231, 232) was carnivorous, with a differentiated dentition, including large canine tusks; the second type, to which belonged *Tapinocephalus, Moschops, Delphinognathus* (Fig. 232, *C*), and other forms, was herbivorous, with small teeth. Both types are fairly common in the Middle Permian Karroo beds. Almost all were large forms; dinocephalians were the largest of mammal-like reptiles and, indeed, the largest-known Permian animals of any sort, being rivaled in size only by the contemporary pareiasaurs. These last probably furnished the main food supply of the carnivorous dinocephalians, while the herbivores probably competed with the pareiasaurs for plant food. Most of the dinocephalians were off the line leading to later therapsid types, but some early Russian types may be very close to the common ancestry of the order.

Dicynodonts.—Most aberrant but temporarily most successful of therapsids were the "two-tuskers" of the suborder Dicynodontia. They appeared in the Middle Permian, and in late Permian times were by far the commonest of all reptiles. They were present not only in South Africa but in the Upper Permian in Russia and Scotland; and in the Triassic, dicynodonts were present in Asia and both Americas.

The dentition was peculiar. In a few of the more primitive types there were small molars; but in most cases there remained only the tusklike upper canine teeth, and even these were apparently restricted to the males in most genera. The jaws obviously were covered by a horny beak similar to that of turtles.

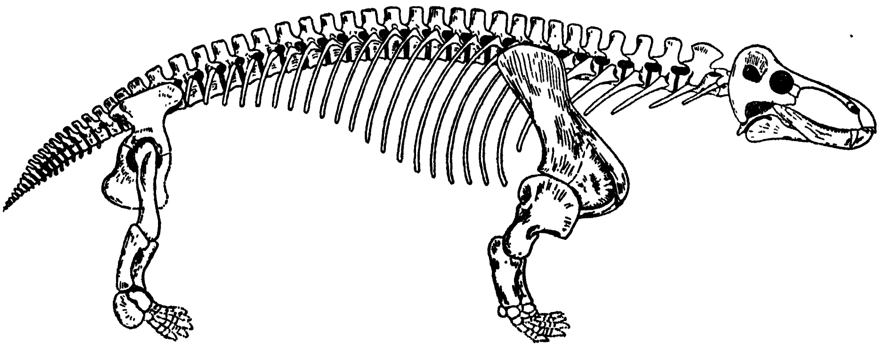


FIG. 231.—The skeleton of the dinocephalian *Jonkeria;* length of original about 14 feet. (After Broom.)

The skull was considerably specialized, rather broad and flat, with an odd arched construction of the cheek region. There was an incipient secondary palate, and other advanced features were present. The postorbital and squamosal, however, still met above the temporal opening. The postcranial skeleton was of an advanced character and resembled that of such a form as *Cynognathus* in many features, although the limbs were rather short and stubby. Here the phalangeal formula was reduced to the mammalian count of 2–3–3–3–3.

The dicynodonts appear to have been marsh-dwelling herbivores; one type—*Lystrosaurus*—appears to have been somewhat aquatic in habits and has been called a "reptilian seal." They ranged in size from species with a skull not more than an inch or two in length to forms with a skull 3 feet long.

Many of the varied Permian types are included in the genus *Dicynodon* (Fig. 232), with more than fifty described species. *Kannemeyeria* (Fig. 233) was one of a number of large Triassic survivors. These harmless plant-feeders seem to have held out well against their carnivorous relatives but disappeared with the advent of large flesh-eating archosaurians in later Triassic times.

Advanced therapsids.—The more progressive members of the order were the dominant reptilian carnivores of the late Permian and the early part of the Triassic. These forms were active flesh-eaters of medium or small size with a differentiated dentition and a rather mammal-like limb structure. In the Permian and Lower Triassic they were abundant in Beaufort beds of the South African Karroo, and they are represented in the Russian Permian and the Triassic of Brazil. All these carnivores have many features in common and are generally regarded as constituting a single suborder—the Theriodontia. There are, however, several subgroups of theriodonts, readily distinguishable from one another. These include (1) the Gorgonopsia, including very primitive forms; (2) the Cynodontia, progressive types; (3) the Thero-

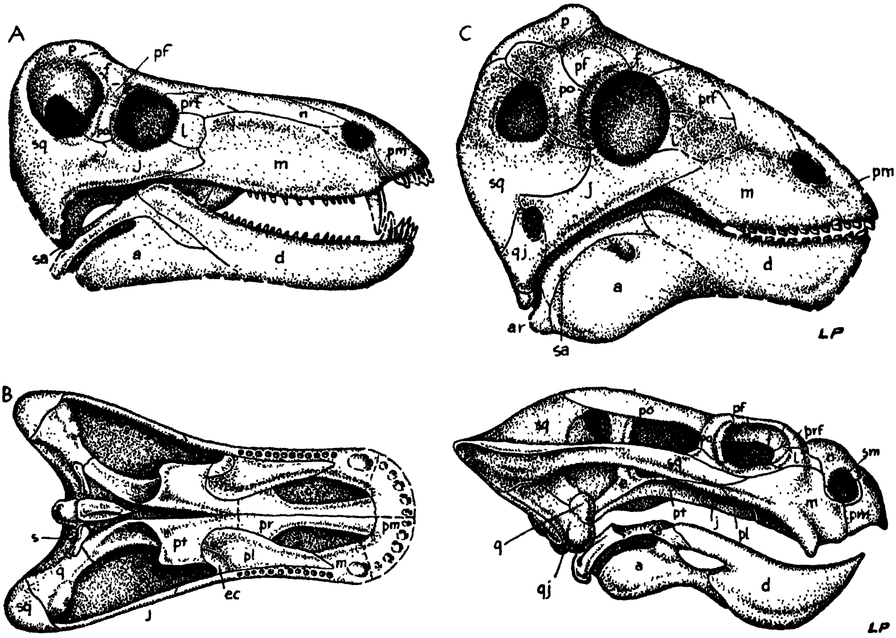


FIG. 232.—*A–C*, The skulls of dinocephalians. *A*, Lateral view of *Jonkeria*, skull length about 29 inches; *B*, palatal view of the same; *C*, lateral view of skull of *Delphinognathus*, length about 15 inches. *Lower right*, the skull of *Dicynodon kolbei*. For abbreviations see Figure 96. (After Broom.)

cephalia, advanced members of which are sometimes separated as the Bauriamorpha.

The gorgonopsians, such as *Scymnognathus* (Fig. 234), were perhaps the most primitive of these carnivores and were common in Middle and Upper Permian times. There were many primitive features in the group. The postorbital and squamosal still met above the temporal opening; the postfrontal bone was still present; there was no secondary palate, although the vomers had fused into a single bar; the condyle was still single; the dentary, although large and with an ascending branch, does not greatly exceed the other elements in size; the postcranial skeleton was somewhat more primitive and more heavily built than in the cynodonts; the phalangeal formula was still 2–3–4–5–3, although the "extra" joints were small.

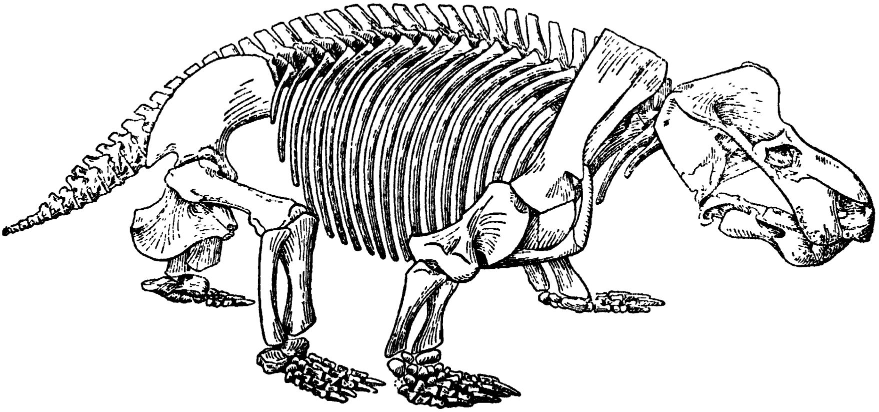


FIG. 233.—The skeleton of *Kannemeyeria*, a Lower Triassic dicynodont; length about 6 feet. (From Pearson.)

Cynognathus, described above, was a typical member of the Cynodontia. This group is often considered to be derived from the gorgonopsians (although descent from the therocephalians is also advocated) but shows many advanced features, particularly in the construction of the palate and jaws. The cynodonts were the common early Triassic carnivores. There was considerable variation in size, the smallest cynodont being not much bigger than a rat, the largest the size of a wolf. The posterior, or cheek, teeth of cynodonts varied widely. In contrast with most other therapsids, the teeth usually had several cusps, and in some cases a grinding surface or crown had developed much as in mammals.

The therocephalians (Fig. 234) were contemporaries of the gorgonopsians and resembled them in many features. But they were already in advance of either gorgonopsians or cynodonts in one respect, for they had attained the mammalian phalangeal formula of 2–3–3–3–3 (Figs. 226, *C;* 227, *C*). In typical members of the Therocephalia, characteristic openings are present perforating the palate posteriorly. Therocephalians are common in the Middle and Upper Permian. In the Lower Triassic, *Bauria* (Fig. 235) and other genera descended from the Permian therocephalians had become as advanced as the cynodonts and, indeed, even more so; for in some members of this group the bar behind the orbit had broken down, as in primitive mammals, and the pineal eye had disappeared. However, these forms were less progressive than the cynodonts in other respects, such as the comparatively large size of many of the bones of the back of the jaw. The structure of the palate indicates that they were evolved therocephalians and that the advanced features which they share with cynodonts had developed independently in the two groups.

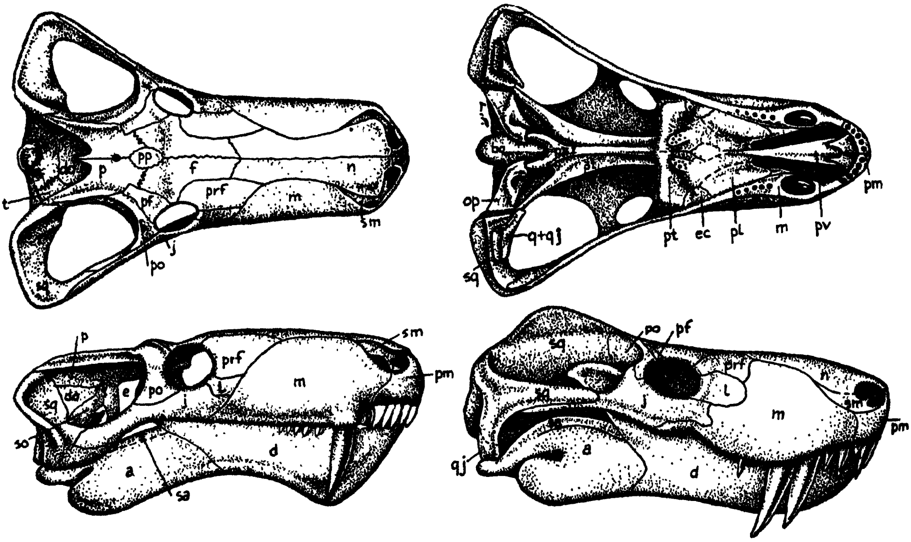


Fig. 234.—The skull in primitive theriodonts. *Upper left*, dorsal view of the skull of the gorgonopsian *Scymnognathus*, length about 1 foot; *upper right*, palatal view; *lower left*, lateral view. *Lower right*, lateral view of the skull of the therocephalian *Lycosuchus*, length about 11 inches; *pp*, preparietal; *so*, supraoccipital. For other abbreviations see Figure 96. (After Broom and Watson.)

Therapsid history.—In the varied therapsid types we span nearly the entire evolutionary gap between a primitive reptile and a mammal. In the skull the more primitive pelycosaurs had few features (apart from the small lateral temporal opening) not present in cotylosaurs; but in one group or another of the more advanced therapsids almost every diagnostic feature of mammals had been attained. A considerable number of bony elements had been lost, the pineal eye had been eliminated, the quadrate and quadratojugal were much reduced, the temporal opening had expanded, and the bar behind the orbit sometimes disappeared. The occipital condyle was double in higher types as in mammals, and the palate had evolved strongly in a mammalian direction. The jaw elements were never reduced to the dentary alone, as in a mammal; but the other elements had become quite small. The teeth were differentiated into incisors, canines, and molars, much as in mammals.

The limb skeleton, too, approached the mammalian condition (cf. Figs. 222–27). The pelycosaurs still had the primitive type of limb, with the proximal elements held out horizontally from the body. In the higher therapsids the limbs had swung around practically into the fore-and-aft position of the mammals and had gone through a series of structural changes which was a logical consequence of this changed posture; these changes included such features as the development of a spine and acromion on the scapula, a forward growth of the ilium, the development of an opening between pubis and ischium, and the reduction of the phalanges in some types to a formula of 2–3–3–3–3. The skeleton of the advanced therapsids was almost as mammal-like as that of such a primitive mammal as the duckbill of Australia.

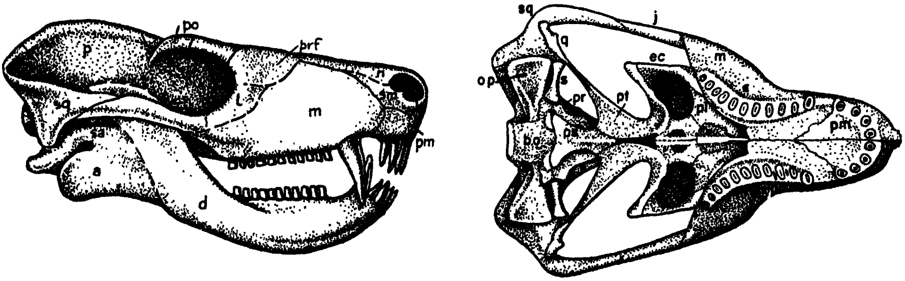


FIG. 235.—*Bauria*, an advanced theriodont, lateral and palatal views of the skull; length about 6 inches. For abbreviations see Figure 96. (After Broom and Boonstra.)

We have noted that such mammalian characters as the reduction in phalanges and the formation of a secondary palate have been independently acquired in several therapsid groups. The cynodonts are sometimes thought to be mammalian ancestors, but there are minor features which tend to debar them from such a position. *Bauria* in some features is closer still but may likewise prove to be somewhat off the path. But, although the details of the phylogenetic history are still uncertain, the therapsid ancestry of mammals seems established.

Ictidosaurians.—By late Triassic times the typical therapsids had apparently become extinct. In the mid-Jurassic there appear forms which can be definitely classified as mammals. Between, there lies an evolutionary "no-man's land," a time when the transition from reptiles to mammals was occurring. Unfortunately, our knowledge of this transition is poor. There are specimens from the late Triassic of South Africa, others from equivalent

(Rhaetic) beds in Europe, and a few more from the Upper Triassic of North America and Asia. These specimens, however, are few in number, fragmentary in character, and puzzling in nature. Some have been referred to at times as primitive mammals, some as advanced therapsids. We shall here, provisionally and arbitrarily, include these seemingly transitional types in an order Ictidosauria as a final stage in synapsid evolution toward the Mammalia.

The reasons for our difficulties in interpretation and classification of this fragmentary material are apparent. Many of the diagnostic features of the mammals lie in their soft anatomy and reproductive processes, and there is little or nothing to be learned of such matters from fossils. In the skeleton we have seen that the advanced therapsids have already bridged most of the gaps between the typical reptilian organization and that of the Mammalia. It is generally agreed that the dividing line may be reasonably established, osteologically, at the point where the "extra" jaw elements are lost and the dentary articulates directly with the skull. But these postdentary elements are already small in advanced therapsids; and, unless the material is well preserved, their presence or absence is difficult to determine. Apart from

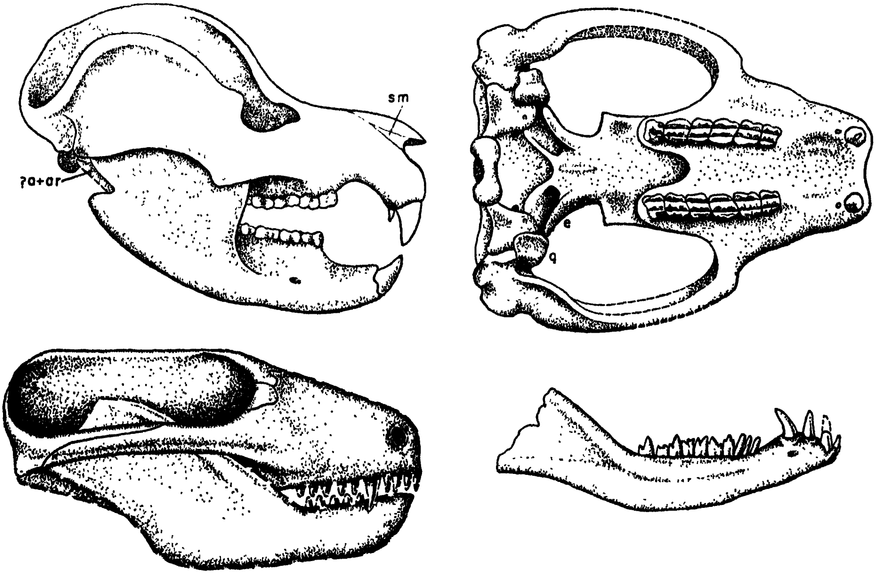


FIG. 236.—Ictidosaurians. *Above,* lateral and palatal views of the skull of *Bienotherium,* a tritylodontid from the Triassic of China; length of original about 5 inches; *a+ar,* angular+articular; *sm,* septomaxilla. (After Young and Watson.) *Lower left,* a small Triassic ictidosaurian from South Africa. (After Broom.) *Lower right,* jaw of *Dromatherium* from the late Triassic of North Carolina; length of original about 1½ inches. (After Simpson.)

this, there are but a few features in the teeth and skull structure which appear to be of use as distinguishing characters.

A few of these problematical forms may be given brief mention. In Figure 236 is seen the skull of a small form from the late Triassic of South Africa. In this type, as in some of the bauriamorphans, the pineal opening had been lost, and the bar behind the orbit had broken down; and, further, not only the postfrontal but the prefrontal and postorbital, in addition, had disappeared from the circumorbital series of bones, leaving the skull roof in an essentially mammalian condition. A secondary palate had developed, as in advanced therapsids, but was here much more like that of mammals. Practically the only diagnostic reptilian character remaining was the fact that some of the extra jaw elements (angular, surangular, articular, and prearticular) appear to have been present, although exceedingly small. While the postcranial skeleton is poorly known, it appears to have been very mammal-like.

Also close to the mammals appear to have been *Dromatherium* (Fig. 236) and *Microconodon*, known only from two jaws from the Triassic of North Carolina. These jaws are about an inch in length and, as preserved, consist of a dentary bone alone. There were three incisors, a canine, and about ten cheek teeth. The teeth of the molar series had elongated, narrow crowns with a large central cusp and accessory cusps on the slopes of the main one. It was long held that these forms were true mammals with but a single bone in the jaw rather than the seven reptilian elements; and this belief was reinforced by the fact that there were thought to be two roots to the molar teeth. Recently, however, it has been shown that the roots were not yet truly divided and that, although the dentary was large, there were very likely other jaw elements present in life.

Still more puzzling in many ways is a group including *Tritylodon* of South Africa and Europe and *Bienotherium* (Fig. 236) of China, both of the late Triassic or earliest Jurassic. These were by no means primitive types, for there were specialized pairs of enlarged incisors and multicusped molar teeth. Such a dental battery is found in mammals among the multituberculates (cf. Fig. 253) and marsupials, and *Tritylodon* was long thought to be a multituberculate and the oldest-known mammal. Recent discoveries, however, include skulls of *Bienotherium* which show suggestive reptile-like characters, and jaw materials of *Tritylodon* or a related genus which indicate that the old reptilian elements were present in the jaws. The multituberculate resemblances are merely parallelisms; the tritylodonts are, it seems, one of many "experiments" among these advanced reptiles in the development of mammalian characteristics.

CHAPTER 15

THE STRUCTURE OF MAMMALS

WE NOW enter upon a consideration of the mammals, the most intelligent and the most successful of land vertebrates. Arising, we believe, at about the end of the Triassic from the mammal-like reptile stock, the group remained comparatively unimportant until the extinction of the great reptiles at the end of the Mesozoic. From that time on, however, mammals increased rapidly in numbers and diversification, so that now they include the greater part of the animals with which one is ordinarily familiar. They not only inhabit the surface of the earth but have invaded the air (bats) and returned to the seas (whales, seals, sirenians). In size they range from tiny shrews and mice to certain of the whales which are the largest of all known animals, exceeding even the greatest dinosaurs in size. Mammals are of particular interest to man, not only because they include many of his animal friends and enemies and much of his food supply, but also because he himself is a member of this group.

Diagnostic characters.—Many of the diagnostic features of mammals lie in their soft anatomy and hence cannot be used in paleontology. As the name implies, they alone among vertebrates suckle their young after birth. There is thus a period of infancy and "education" which, it would seem, enables mammals to make better use of their finer physical and mental equipment. The young are, except in the most primitive forms, born alive, the shell-less egg being retained within the mother's uterus. The yolk dwindles, and in most cases a connection, the placenta, is formed by which the young can be nourished by transfusion between the blood streams of the mother and the young. Mammals are warm blooded, that is, they maintain a high body temperature with a consequent potentiality of maintenance of continuous activity; the presence of hair (apparently originally developed between the scales) aids in the preservation of the body heat. Horny scales are only rarely present; superficial dermal ossifications are uncommon. There is a four-chambered heart, as in birds, with a perfect separation of the pure and the impure blood, and only one arch of the aorta; but, whereas in birds the arch is the right, here it is the left.

The brain is much enlarged (Fig. 237), the growth of the higher centers in the cerebral hemispheres being the most characteristic change; the hemispheres grow upward and backward, cover the midbrain and often overlie the cerebellum, and usually further increase their area of superficial gray matter by an infolding of the surface. In the brains of the higher mammals the entire dorsal surface of the cerebrum represents a new outgrowth and infolding of nervous tissue, collectively called the neopallium or "new brain"; this has overgrown the old brain, forming a "supercontrol" system that dominates the old vertebrate brain beneath it. By its means memory is greatly enriched, and the animal is enabled to make a more or less intelligent choice between conflicting sensory stimuli, so that it can be guided by memory of past reactions and their results. It is of interest that in many groups of mammals (the horses, for example) there was a strong tendency for brain growth during Tertiary times; the older members of such groups had relatively much smaller brains than their late Tertiary and modern representatives. Activity guided by intelligence is the keynote of mammalian success, contrasting with the sloth and stupidity of reptiles. The warm-blooded condition has rendered possible the activity without which the many skeletal adaptations of mammals would be useless; the mammalian mode of development has rendered possible the ontogenetic elaboration of the complicated brain structure.

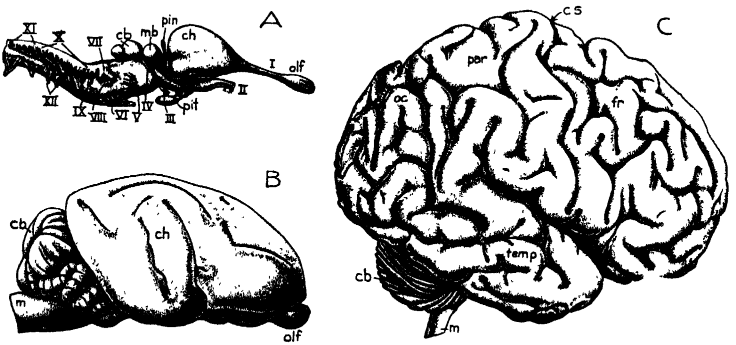


FIG. 237.—The brain in *A*, a reptile (alligator); *B*, a lemur; *C*, a human (newborn child). In all, the brain stem is drawn at about the same actual length; the enormous increase in the relative size of the cerebral hemispheres (*ch*) may be noted. In the alligator the cranial nerves are numbered. Abbreviations: *olf*, olfactory bulb; *pin*, pineal eye; *mb*, midbrain region, with optic lobes above; *pit*, pituitary; *cb*, cerebellum; *m*, medulla oblongata.

In the cerebral hemispheres of man the various lobes—frontal, parietal, occipital, and temporal—are indicated, as well as the central sulcus (*c.s.*) dividing the motor area from the sensory area behind it.

Among osteological characters which are usually considered as diagnostic are the following: the double condyle of the skull; the presence of epiphyses on certain, at least, of the bones; only one element (dentary) on each side of the lower jaw, this element articulating with the squamosal; the tympanic membrane supported by a tympanic bone; the presence of three auditory ossicles; the presence of only marginal teeth in the jaws; two definite tooth generations; two or more roots in the cheek teeth; and a single bony nasal opening. Some of these characters, however, were already present or foreshadowed in the therapsids.

Skeleton.—The study of the skeleton in mammals presents an entirely different problem from that encountered in the reptiles. In that class there is an extremely wide variation in skeletal patterns and in the elements present. The mammalian skeleton has evolved from the type seen in the mammal-like reptiles and thus is, in a sense, highly specialized to begin with. Once established, however, it has varied but little. Almost never are new skeletal elements added, and seldom are elements lost, except in the distal portions of the limbs in relation to locomotor adaptations. But, although the bones of the skeleton are essentially stabilized, tooth structure is, as will be seen, exceedingly variable. Teeth are, from their composition, the hardest of skeletal materials and the parts most frequently preserved as fossils. In consequence, dentition and limb structure, as the two most variable and diagnostic features of the mammalian skeleton, will bulk large in our consideration of the various groups.

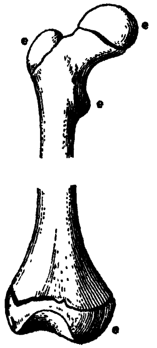


FIG. 238.—A mammalian femur at an immature stage. (For economy of space much of the shaft has been omitted.) The two articular regions and the principal points of muscular attachment long remain as separate pieces of bone—epiphyses (*e*)—between which and the shaft there remain areas of cartilage in which new bone may form.

The mammalian skeleton contrasts with that of reptiles in its thorough ossification; exceedingly little cartilage is present in the adult. One development in this regard deserves particular mention—the epiphyses (Fig. 238). In reptiles the articular ends of bones are frequently covered by cartilage; growth in length of the bones takes place by the gradual replacement of this cartilage by bone. Such a process, however, hinders the development of a firm articulation of one element with another. In mammals this difficulty has, so to speak, been solved: the articular surface is formed of bone and finished early in life. But between the ends and the main body of the bone there is a layer of cartilage in which additional bone is laid down. Lengthening of a bone may thus take place without interference with its articulations. When the element has reached its maximum size, this zone of cartilage disappears, and the end-segments, known as epiphyses, fuse with the main body of the element. After their fusion, growth is over. This is in contrast with typical reptilian conditions, in which no definite adult size is attained and growth may continue, seemingly, throughout life; epiphyses are rarely present.

Skull.—The interpretation of the mammalian skull (Fig. 239) is rendered easier if the reptilian ground plan upon which it is based is kept in mind. It is a highly complex structure, differing from that of therapsids mainly in features connected with the great expansion of the brain and with changes in the nasal apparatus and the auditory mechanism.

As seen in dorsal view, the greatest change from the reptilian condition is that caused by the growth of the brain and the consequent swelling-out of the braincase; the temporal arches stand out from the sides of the skull as if they were appendages to it rather than part of the original roof. There is no pineal eye, and the bony external nares are fused into a common anterior opening. There is the normal tetrapod series of parietals, frontals, nasals, and premaxillae. The parietals spread down over the sides of the braincase. If the brain is small, the jaw muscles meet above, causing a median sagittal crest to develop between them. This structure is most likely to be present in large forms, for the brain does not increase in proportion to the rest of the body. There is no bar behind the orbit in primitive mammals, and the reptilian postorbital bone is gone. The bar may re-form in advanced members of many groups, but this bone does not return. The prefrontal and postfrontal are likewise absent; the lacrimal is small and confined to the neighborhood of the orbit and the tear duct. In front, the nasals project freely over the nares; and the premaxillae push up to meet the nasals on either side. The maxillae are large and deep, as they were in mammal-like reptiles. The jugal lies beneath the orbit and takes part in the formation of the temporal arch. The squamosal forms the hinder end of this bar and also the new jaw articulation—the glenoid cavity—as well as extending up over the lateral wall of the braincase. In contrast to reptiles, quadratojugal and quadrate are absent from their former place at the back corner of the skull.

As in reptiles, there is usually a considerable amount of fusion of the elements which make up the occipital plate. The basioccipital, lying below the foramen magnum, is fused with the exoccipitals. The latter form much of the paired condyles, extend out laterally into paroccipital processes, and may fuse in turn with the supraoccipital. Embryology often reveals a distinct postparietal (dermal supraoccipital) which usually fuses with the supraoccipital. There is usually a transverse (lambdoidal) crest across the upper margin of the occiput for the attachment of neck muscles.

On the under side of the braincase the basisphenoid lies in front of the basioccipital, bounded posterolaterally by the auditory region and internally containing a cavity (sella turcica) in which the pituitary body is lodged. At the side of the basisphenoid is the alisphenoid, which extends up as a wing around the side of the braincase and meets the roofing bones above. This appears to have been derived from the epipterygoid—a bone of the upper-jaw region of lower vertebrates, here pressed into service to cover what otherwise would have been a gap in the wall of the expanding mammalian braincase. Anterior to the basisphenoid is the presphenoid, which forms the most anterior part of the floor of the brain cavity. On either side is a plate of bone termed the orbitosphenoid, but which is continuous with presphenoid and essentially a part of it. These bones are seemingly derived from the reptilian (and amphibian) sphenethmoid. Still farther forward in the brain-

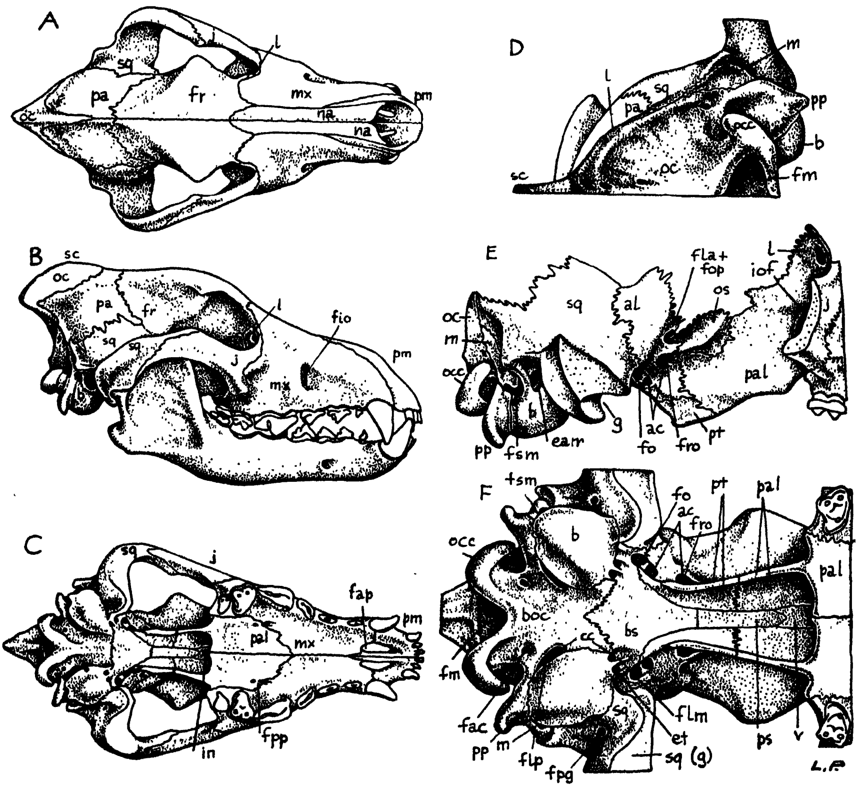


FIG. 239.—The skull of the Pleistocene wolf, *Canis dirus*, to show the structure of the mammalian skull. *A*, Dorsal, *B*, lateral, and *C*, ventral views. *D*, Occipital view of right half of skull (top at left of figure). *E*, Lateral view of posterior part of skull with zygomatic arch and roofing bones removed. *F*, Ventral view of same. Abbreviations: *ac*, alisphenoid canal; *al*, alisphenoid; *b*, auditory bulla; *boc*, basioccipital; *bs*, basisphenoid; *cc*, carotid canal; *eam*, external auditory meatus; *et*, Eustachian tube; *fac*, anterior condyloid foramen; *fap*, anterior palatine foramen; *fio*, infraorbital foramen; *fla*, anterior lacerate (sphenorbital) foramen; *flm*, median lacerate foramen; *flp*, posterior lacerate foramen; *fm*, foramen magnum; *fo*, foramen ovale; *fop*, optic foramen (here fused with *fla*); *fpg*, postglenoid foramen (transmitting a nerve); *fpp*, posterior palatine foramen; *fr*, frontal; *fro*, foramen rotundum; *fsm*, stylomastoid foramen; *g*, glenoid fossa (jaw articulation); *in*, internal nares; *iof*, infraorbital foramen; *j*, jugal; *l*, lacrimal carrying tear duct, also lamboidal (transverse occipital) crest; *m*, mastoid portion of periotic; *mx*, maxilla; *na*, nasal; *oc*, occipital (including basioccipital, exoccipital and supraoccipital); *occ*, occipital condyle; *os*, orbitosphenoid; *pa*, parietal; *pal*, palatine; *per*, periotic; *pm*, premaxilla; *pp*, paroccipital process of exoccipital; *ps*, presphenoid; *pt*, pterygoid; *sc*, sagittal crest; *sq*, squamosal; *v*, vomer.

case of many mammals there lies, at the hind end of the nasal chamber, a mesethmoid element. From this element and from the inner portions of the nasals and maxillae, scrolls of bone extend into and subdivide the nasal cavities. These are the turbinals which are covered in life with mucous membranes.

In the front part of the mouth the bony structure is not unlike that of the higher therapsids. The secondary palate is formed by extensions from the premaxilla, maxilla, and palatine back to the internal nares. Behind the palatine is the pterygoid, closely articulated to the basicranial region. It no longer reaches back to the quadrate region and ends behind in a winglike structure. (The ectopterygoid has vanished.) Below the braincase, in front of the presphenoid and partially concealed from ventral view by the secondary palate, is a long, slim median bone, of dermal origin—the vomer. This is probably derived by fusion from the paired elements to which we have applied this name in lower vertebrates (although another theory would derive the vomer from the reptilian parasphenoid).

Auditory region.—The capsule inclosing the inner-ear region in reptiles and primitive amphibians (cf. Fig. 96) was formed of two bones—proötic and opisthotic—usually fused, lying well back in the lateral wall of the braincase, and having a lateral opening (fenestra ovalis) on the outer surface, with which the stapes articulated. In mammals these bones have fused into a single compact structure—the petrosal. This is in contact posteriorly and ventrally with the occipital complex and is covered superficially in great measure by the squamosal. The petrosal is frequently exposed, as the mastoid process or region, at the posterolateral margin of the skull between these two adjacent elements.

In mammals the eardrum tends to be surrounded and supported by a small bone termed the tympanic, primitively a ring-shaped or horseshoe-shaped structure, which is thought to be a remnant of the angular bone of the reptilian lower jaw. Between eardrum and otic capsule in mammals is the air-filled middle-ear cavity, containing the delicate auditory ossicles discussed below. There is a tendency in most mammalian groups for this cavity to be surrounded by bone, which may form an auditory bulla. This fuses with the petrosal, the fused mass being termed the periotic. The bulla is, however, formed in somewhat variable fashion. The tympanic bone may grow inward from the eardrum to form the entire structure; in many forms, however, a new element, termed the entotympanic, not present in any reptile, takes part in bulla formation.

Skull openings.—The various openings in the skull (foramina and fenestrae) are numerous, complicated, and important. They may be roughly divided into (1) openings out of the braincase for cranial nerves and (2) openings for blood vessels and various ducts.

Mammals possess twelve cranial nerves, passing directly from the brain to the sense organs and muscles of the head and throat. We shall briefly list these and their more usual relations to the skull openings (Fig. 239, *E*, *F*). Nerve I, the olfactory, reaches the nasal chamber by perforating the anterior end of the braincase in the ethmoid region. Nerve II, the optic, passes out to the eye through the optic foramen in the orbitosphenoid. The three small nerves to the muscles of the eye (III, IV, VI) and part of the large nerve V (trigeminal) pass out through the foramen lacerum anterius (or foramen sphenorbitale) between orbitosphenoid and alisphenoid inside the cavity of the orbit. Two other branches of nerve V pass out through the foramen rotundum and foramen ovale, both in the alisphenoid bone. Nerve VII (facial) passes through the petrosal and emerges at the edge of the skull from the stylomastoid foramen. Nerve VIII, the auditory nerve, passes into the petrosal to the inner ear and does not, of course, reach the surface of the skull. Nerves IX, X, and XI (glossopharyngeal, vagus, and accessory) pass out through the posterior lacerate or jugular foramen between the basioccipital and the ear capsule, while XII (hypoglossal) sometimes accompanies them but originally emerged through an anterior condyloid foramen in the exoccipital.

The lacrimal duct usually pierces the lacrimal bone at the anterior edge of the orbit and runs inward to reach the nose. An infraorbital canal carries blood vessels and nerves forward from the orbit through the maxilla into the face. On the palate the incisive foramina between premaxilla and maxilla have openings into the mouth in many mammals for Jacobson's organ (absent in man)—an accessory nasal pouch for smelling mouth contents; farther posteriorly the palatine foramina transmit blood vessels. There is often an alisphenoid canal carrying an artery forward through the base of the alisphenoid bone. The internal carotid artery which supplies blood to the brain usually passes forward from the hind end of the skull through a carotid canal running forward under cover of the petrosal from near the posterior lacerate foramen, while at the front end of that bone the artery passes up into the braincase through the foramen lacerum medium, an opening between petrosal and alisphenoid. In this region there is an opening into the auditory bulla for the Eustachian tube leading from throat to middle ear. In the jaw there is a foramen (inferior dental) on the inner side near the posterior end through which enter nerves and blood vessels, and a mental foramen well forward on the outer side to give a blood and nerve supply to the chin and lower-lip region.

Jaw and auditory ossicles.—In the lower jaw there is but a single element on each side—the dentary. This has an ascending ramus with a coronoid process (for the temporal muscle which closes the jaw) and an articular process. At the lower back corner of the jaw there is often an angular process for the attachment of muscles.

Of the other elements of the reptilian jaw (cf. Fig. 230), the splenial, coronoid, and surangular seem to have disappeared in mammals. The angular has become the tympanic bone. This leaves the articular (with which the prearticular is fused) and, in the upper jaw, the quadrate (to which in mammal-like reptiles the quadratojugal was fused). The fate of these two bones has been a curious one.

In mammal-like reptiles the sole auditory ossicle—the stapes—ran out to touch the quadrate; this element, in turn, was in contact with the articular bone of the jaw. In the mammalian auditory region this "stirrup bone" is the inner member of a chain of three ossicles, an outer one—the malleus or "hammer"—receiving vibrations from the eardrum and transmitting them to the stapes through the incus or "anvil." The origin of these two "new" elements was long disputed. But a study of their embryology confirms the conclusion to which a consideration of the jaw changes undergone in the evolution of mammals leads us. The malleus is the old articular; the incus, the reptilian quadrate. Once important bones, they had become useless for their original purpose and, lying close to the auditory region, were salvaged and put to a new use. This change was presumably facilitated through the fact that in the mammal-like reptiles the eardrum lay close to the jaw region. Very likely quadrate and articular had begun to function in sound transmission before they had lost their function as jaw elements.

The history of the auditory ossicles is one of the best examples of a change of function to be found in vertebrates. These elements, it will be recalled, were once part of the shark jaw apparatus; and this, in turn, was derived originally from branchial bars. Accessory breathing organs were transformed into biting structures and these, finally, into part of the hearing apparatus.

Some portions of the reptilian branchial apparatus, especially the hyoid, remain in the tongue and throat of mammals, but they are paleontologically unimportant.

Dentition.—Teeth in mammals are confined to the margins of the jaws. They consist (Fig. 240) of incisors, canines, premolars, and molars. In the upper jaw the incisors are in the premaxilla, the others in the maxilla. All the teeth except the molars have, normally, a "milk" or deciduous set preceding the permanent ones. The deciduous teeth appear, in general, in rather regular order from front to back (although canines with heavy roots may lag a bit in their appearance). When the premolar row has been completed, the molars appear in order, posterior to them. But meanwhile the replacement of the anterior teeth begins again in fore-to-aft sequence. The molars are "permanent" teeth but are actually posterior, unreplaced members of the same set of teeth to which belong the deciduous teeth anterior to them. This tends to explain the fact that in many cases the "milk" premolars are more like the molars than are the permanent teeth which replace them.

In a primitive placental mammal there were three incisors in each half of each jaw. No mammal has more than one pair of canines above and below. Four premolars and three molars in each half of the jaw is the number present in primitive placentals. This set of statements may be written simply as a dental formula, $\frac{3\cdot1\cdot4\cdot3}{3\cdot1\cdot4\cdot3} \times 2 = 44$; and a similar system may be used for any set of teeth. Primitive mammals may have a larger number of teeth; in placentals the formula given is usually the maximum, and there is often a considerable reduction; our own formula, for example, is $\frac{2\cdot1\cdot2\cdot3}{2\cdot1\cdot2\cdot3} \times 2 = 32$.

The incisors are generally nipping teeth of moderate size. In some cases (as in rodents) a pair may be developed as strong chisels, or they become tusks, as in the elephant. The canines are primitively long, stabbing, cone-shaped teeth. They are emphasized in carnivores; in herbivores they may be lost but are sometimes retained as defensive weapons. The cheek teeth—premolars and molars—usually have at least two roots in mammals. The four premolars are primitively simpler in structure than the molars. In many herbivore types they tend to become more complicated and may resemble the molars. In herbivorous mammals the molars tend to take on a complicated pattern, but in carnivores they tend to become reduced.

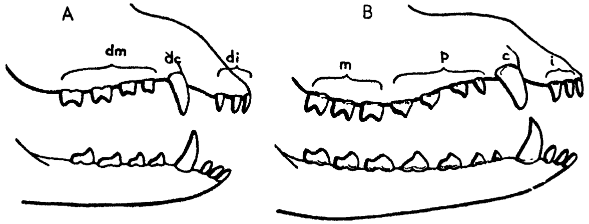


FIG. 240.—Diagrams to show the types and numbers of teeth in a primitive placental mammal. *A*, Deciduous ("milk") teeth. Abbreviations: *di*, deciduous incisors; *dc*, deciduous canine; *dm*, deciduous premolars ("milk molars"). *B*, Permanent dentition. Abbreviations: *i*, incisors; *c*, canine; *p*, premolars; *m*, molars.

In primitive mammals there was a closed tooth row, without pronounced gaps; but herbivores tend to develop a gap, or diastema, between the front teeth which secure the food and the cheek teeth which masticate it.

Cheek teeth were primitively low crowned (brachyodont); but in many large animals or in forms in which there is unusual wear, as in gnawing or grass-eating, they become high crowned (hypsodont). The roots primitively closed, limiting the amount of crown material formed, but in some forms part or all of the teeth may have a continuous growth.

Molar structure.—Reptilian teeth are generally simple cones. Mammalian molars generally have a broad crown bearing a number of cusps or ridges arranged in a complicated pattern which varies widely from group to group. It was only natural that there should have arisen various theories to account for the origin of molar patterns and to homologize the various cusps and crests found in different types. There have been some fantastic theories based on the idea that each cusp represents an originally separate tooth; however, the tritubercular theory set forth below is generally accepted today in at least certain of its aspects.

The theory starts with the type of molar teeth found in many primitive placentals, particularly Paleocene and Eocene forms (Fig. 241). In the upper jaws the molars are triangular in shape, with three major cusps. A single cusp is found at the inner apex; this was once believed to represent the original reptilian cone and hence is called the protocone. External to this is the paracone; back of the paracone is a third, the metacone. Along a ridge leading out and forward from the protocone there is often a smaller cusp, the protoconule (or preferably paraconule); along a similar posterior ridge, a metaconule. Paracone and metacone may be partially joined by ridges. On the outer margin of the tooth there was primitively a prominent shelf, termed a cingulum; and cingula also tended to be present along the margins anterior and (particularly) posterior to the protocone.

In the lower jaw there was a similar triangle, but with the base inside and the apex outside. Similar names are given to these cusps, but with the suffix *-id:* protoconid, paraconid, metaconid. Back of the triangle, or trigonid, is a low extension, the heel or talonid. This bears two cusps—an external one termed the hypoconid and an internal one, the entoconid; in addition, there is often a third, smaller cusp—the hypoconulid. A cingulum is often present along the anteroexternal margin.

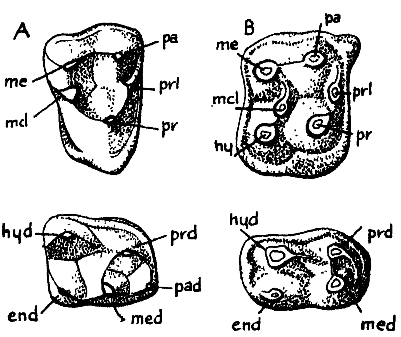


FIG. 241.—Molar teeth of primitive placentals. *Upper row,* right upper molars; *lower row,* left lower molars. *A, Omomys,* a Paleocene tarsioid, with a tritubercular pattern; *B, Hyracotherium,* a Lower Eocene horse, showing the evolved quadritubercular pattern. Abbreviations: upper molars—*hy,* hypocone; *me,* metacone; *mcl,* metaconule; *pa,* paracone; *pcl, prl,* protoconule; *pr,* protocone; lower molars—*end,* entoconid; *hld,* hypoconulid; *hyd,* hypoconid; *med,* metaconid; *pad,* paraconid; *prd,* protoconid. In addition to the cusps shown, primitive lower molars frequently bear a sixth cusp, a hypoconulid, at the posterior margin.

This primitive type of molar tooth, often with fairly sharp cusps, has been termed "tuberculosectorial" or (preferably) "tribosphenic." The triangles are asymmetrical, the front edge of the upper tooth and the hind edge of the lower trigonid being perpendicular to the edge of the jaw. Each upper tooth centers behind its proper lower mate (Fig. 242); and if it were not for the heel below, which received the protocone in its basin, the two teeth would pass each other. A shearing action is obtained by this partial passage, while the partial opposition of the cusps gives a chopping effect.

Mammalian cheek teeth, in contrast to those of typical reptiles, tend to have divided roots. In primitive placental types the upper molars had three roots, one beneath each major cusp, and the lower molars two, one each below trigonid and talonid.

In carnivorous mammals there has been comparatively little change from the generalized condition described above. In herbivorous or mixed feeders, with the development of a grinding surface, the pattern tends to become complicated (Fig. 241). In the upper molars the tooth tends to square itself up, usually by the addition of a fourth cusp, the hypocone, at the inner back corner; the intermediate cusps may remain or drop out. The lower teeth tend also to square up, but in a more complicated way, by building up the heel to a level of the rest of the tooth and dropping the paraconid from the front end so that the four definitive cusps are the protoconid, metaconid, entoconid, and hypoconid.

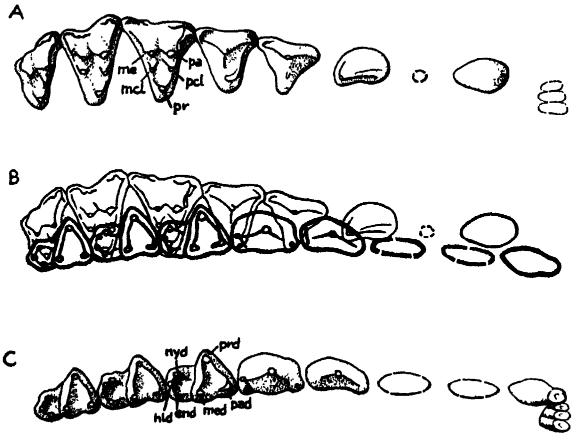


FIG. 242.—Cheek teeth and canines of *Didelphodus*, an Eocene insectivore, to show occlusional relations. *A*, Right upper tooth row; *C*, left lower tooth row; *B*, the two superimposed to show occlusional relations. Each upper tooth lies behind and outside its homologue in the lower jaw. The two rows partially pass each other, with a shearing action along the diagonal line between each upper tooth and the lower tooth behind it. The passage of the upper tooth is stopped by the heel (talonid) on the corresponding lower molar; the protocone fits into the basin of the talonid. For abbreviations see Figure 241. (After Gregory.)

The cusps present may form various types of patterns. They may remain separate but low and rounded—a bunodont (hillock) type of dentition characteristic of such mixed feeders as men and pigs (Figs. 267; 337, *F*, *G;* etc.). Each cusp may tend to expand into a crescent (selenodont type) (Fig. 336, *C-H;* etc.). Rows of cusps may tend to fuse into ridges (lophodont); for example, the two outer cusps of the upper molars may form a ridge, called the ectoloph; an anterior row of cusps may join to form a protoloph; or the back ones may form a metaloph; in lower teeth there may be similar cross-crests termed metalophid and hypolophid (Fig. 243). Vertical ridges, or styles, may form on the edge of the teeth to add to the complication of the pattern.

This tritubercular terminology affords an exceedingly useful method for the description of placental molar teeth. But the theory orginally attempted also to explain the evolution of tritubercular placental teeth from the single-cusped tooth common in reptiles. It assumed that there had developed three cusps in an anteroposterior row, as in the triconodonts described in the next chapter (Fig. 251). Then a rotation of the cusps into the triangular shape seen in the Jurassic symmetrodonts was thought to have taken place; it was assumed that from this condition through the Jurassic pantotheres, or trituberculates, arose the type of tooth found in primitive placentals.

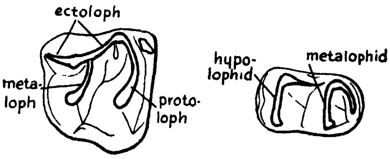


FIG. 243.—Right upper and left lower molars of a fossil rhinoceros, to illustrate a common type of lophodont tooth.

But this part of the tritubercular theory is far from acceptable. In the first place, the triconodonts and symmetrodonts probably have nothing to do with the evolution of the remaining mammals, and there is no evidence of the supposed rotation of the cusps. Further, in the supposed rotation of cusps it was assumed that the original reptilian cone remained at the apex of the triangle, internal above and external below, and it was for this reason that the names protocone and protoconid were applied to the apical cusps. If this were true, it would be expected that this apical cusp, as the oldest historically, would appear first in the embryological development of teeth and that when we trace forward in the tooth row of an animal this cusp would be homologous with the principal cusp of the premolars. This is true in the lower teeth: the protoconid appears to be the primitive reptilian cusp. But in the upper molars the paracone—not the protocone—is the first to appear in tooth development, and it is the paracone and metacone which are in line with the main cusp of the premolars (Fig. 242). Probably, then, the paracone is really the original reptile cusp; the protocone is a newer development at the internal border, while the metacone was formed by splitting off from the paracone.

But while we must divest the names of phylogenetic meaning, it remains true that, starting with a primitive placental, the tritubercular nomenclature is a very valuable tool for the description and comparison of placental molars.

Postcranial skeleton.—The skeletal features of such a generalized mammal as an opossum or certain insectivores are the logical outcome of the adaptations for rapid quadrupedal progression seen in the therapsids; the opossum is a "living fossil," with a skeleton changed but little from the ancestral mammals of the Mesozoic. The reptilian ancestors of the mammals presumably were ground dwellers. But the flexibility of the skeleton of the more generalized mammals and the fact that "thumb" and "big toe" (pollex and hallux) tend primitively to be set off to a slight extent from the other digits, as if some grasping power were early present, suggests a primitive arboreal stage.

In the axial skeleton (Fig. 244) there is greater regional differentiation than in reptiles. Ribless lumbar vertebrae are clearly set off from the rib-bearing dorsals. The cervical region also appears to be ribless, for the ribs are short and fuse in the embryo with the vertebrae. The tail is often long but is merely an appendage, not an integral part of the body, as in most reptiles. The sacral vertebrae tend somewhat to increase in number, and the originally separate sacral ribs tend to be lost and to be replaced by the transverse processes.

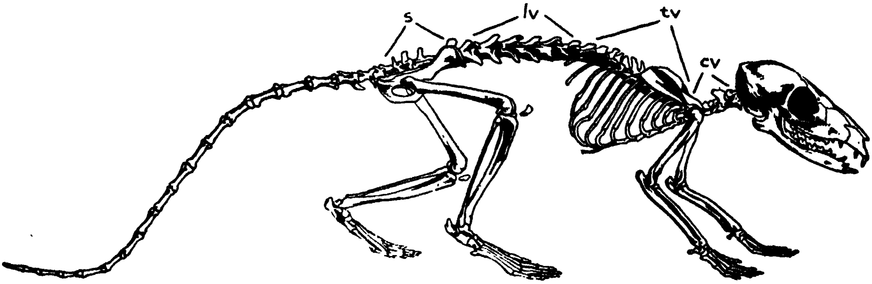


FIG. 244.—Skeleton of the living tree shrew *Tupaia*. Abbreviations: *cv*, cervical vertebrae; *lv*, lumbar vertebrae; *s*, sacrum; *tv*, thoracic vertebrae. (After Gregory.)

The number of vertebrae is much less variable than was the case in reptiles. In general, there are about twenty-five to thirty vertebrae in front of the sacrum. The number of cervicals is almost invariably seven; the long-necked giraffe and the neckless whale differ, not in number of neck vertebrae, but in their proportions. The number of rib-bearing dorsals commonly ranges from about twelve to fourteen, lumbars from five to seven, sacrals from two to five. The caudals are, of course, rather variable; there are rarely as many as two to three dozen. The chief changes from the therapsid condition are seen to be: (1) fusion of the cervical ribs with the transverse processes, (2) loss of ribs in the lumbar region, and (3) tendency for reduction of the tail.

The breastbone, or sternum, unimportant in reptiles, becomes a major feature of the skeleton in mammals. All the longer dorsal ribs attach firmly to it. A tough membrane (the diaphragm) closes off the barrel-like chest region posteriorly. Continued breathing is a necessity for warm-blooded types; this is accomplished by expansion and contraction of the ribs (held together by the sternum) and the diaphragm.

The general contour of the backbone is similar to that of the therapsid ancestors. The cervical vertebrae slant downward from the head. Above the shoulder region, at about the beginning of the dorsal vertebrae, the curve of the back rises, to descend through the lumbar region to the sacrum and tail. The neural spines of the more anterior trunk vertebrae slant backward, those of the lumbar region forward; in the posterior part of the dorsal series there is a transitional (anticlinal) vertebra, whose spine points upward.

The first two vertebrae, the atlas and axis, are of particular interest (Fig. 245). The atlas consists of a ring composed of its own neural arch plus its intercentrum. The axis has, in addition to its own proper elements, the centrum of the atlas attached to its front end as the odontoid process.

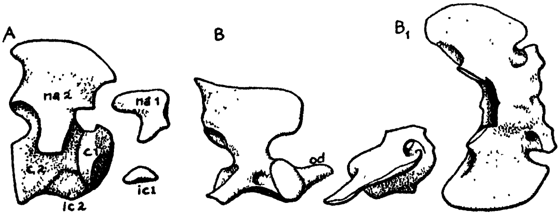


FIG. 245.—The atlas and axis in *A*, the therapsid *Moschops*; *B*, the Oligocene canid *Daphoenus*. Lateral views from right side. B_1, dorsal view of mammalian atlas, posterior end to the left. In both *A* and *B* the two elements are separated. The atlas consists of the neural arch and the intercentrum of the first vertebra (separated in *A*); these form a ringlike structure in mammals (B_1). In mammals the centrum of the first vertebra is fused with the axis as the odontoid process, fitting into the cavity of the atlas. Abbreviations: *c1*, *c2*, centra of the first and second vertebrae; *ic1*, *ic2*, intercentra of same; *na1*, *na2*, neural arches; *od*, odontoid process of axis (=*c1*).

Limbs.—The limbs have continued the rotational process noted in our discussion of the therapsids, so that they lie parallel to the body and almost underneath the trunk. Humerus and femur work in a fore-and-aft plane (Fig. 246), functioning as a type of lever with the fulcrum (knee or elbow) at one end, the weight to be raised near the other end at the articulation with the girdle, and the major force (muscles) attached just beyond at the very tip (greater tuberosity of the humerus, greater trochanter of the femur). The chief muscles are, consequently, dorsal in position, and therefore the limb girdles tend to be reduced ventrally and expanded above. This is particularly marked in the shoulder girdle (Fig. 222, *D*). In typical mammals the interclavicle and the two ventral coracoids have disappeared except for a nubbin of the posterior (true) coracoid element underneath the scapula. The spine of the scapula with which the clavicle articulates is in reality its old front edge; the region anterior to the spine is a new development, an addition on the front for the accommodation of muscles moving up from the coracoid. In the pelvis, too (Fig. 223, *D–F*), there has been a rotation of bone related to rotation of muscles; and the ilium extends far forward, not at all back, while the pubis and ischium are as much behind as below the acetabulum.

The humerus and femur have, of course, changed considerably from the primitive condition because of their rotation. The humerus (Fig. 224, *D*) has, near its proximal end, greater and lesser tuberosities for attachment of the muscles connecting it with the body; distally the primitive reptilian entepicondylar foramen is often present. The femur (Fig. 225, *C*) has greater and lesser trochanters proximally for muscular attachment and often has a third trochanter more distally (a useful diagnostic character in many cases). In carpus and tarsus we lose, unfortunately, the simple and logical reptilian names for the elements and have to adopt a series of individual ones which vary considerably from author to author. In the carpus (Fig. 247, *B*), instead of radiale, intermedium, and ulnare, we speak of scaphoid, lunar, and cuneiform, while an accessory bone on the outer side is called the pisiform. The centrale retains its name, while the four distal carpals are, in order, the

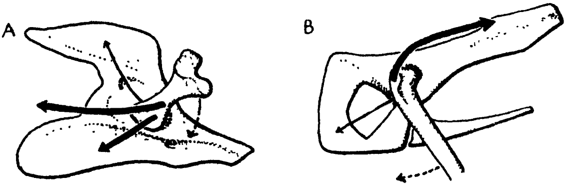


FIG. 246.—Diagram to show the differences in the musculature of the hip region between a pelycosaur (*A*) and a mammal (*B*). In *A* the principal muscles pulling the femur downward and backward (shown in heavy lines) attach to the tail and ventral part of the pelvic girdle. In *B* these muscles are reduced and replaced to a considerable extent by muscles attached to the greater trochanter and inserting on the ilium.

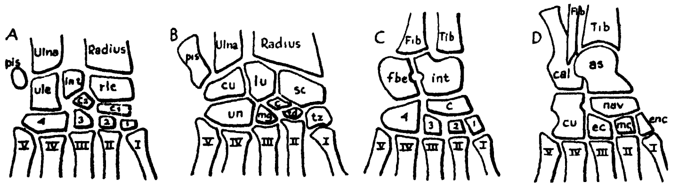


FIG. 247.—Diagrams to show the contrast in nomenclature of the carpal and tarsal elements in mammals and reptiles. *A*, Carpus of reptile; *B*, carpus of mammal; *C*, tarsus of reptile; *D*, tarsus of mammal. Metacarpals and metatarsals in Roman numerals, distal carpals and tarsals of reptiles in Arabic. Abbreviations: *as*, astragalus; *c*, centrale; *cal*, calcaneum; *cu*, cuboid; *ec*, ectocuneiform; *enc*, entocuneiform; *fib*, fibula; *fbe*, fibulare; *int*, intermedium; *lu*, lunar; *nc*, mesocuneiform; *mg*, magnum; *nav*, navicular; *pis*, pisiform; *rle*, radiale; *sc*, scaphoid; *td*, trapezoid; *tib*, tibia; *tz*, trapezium; *un*, unciform; *ule*, ulnare.

trapezium, trapezoid, magnum, and unciform. In the tarsus (Fig. 247, *D*) the intermedium and fibulare are termed the astragalus and calcaneum. The former develops a rolling joint over which the tibia moves freely; the latter projects back as a prominent heel bone to which the calf muscles attach. The distal tarsals become the internal, middle, and external cuneiforms and the cuboid. The primitive phalangeal formula is that which we have seen develop in some mammal-like reptiles, namely, 2–3–3–3–3 (Fig. 248). The pollex and hallux are usually somewhat shorter and thicker than the other toes and diverge somewhat from them, suggesting a grasping power in the primitive mammals. The feet in primitive forms presumably were armed with sharp claws.

Locomotor adaptations.—From the type of skeleton described above, there have been wide variations. Locomotor adaptations to different modes of life are varied and often striking. Among ground dwellers, fast running has evolved in many different groups. The beginning of such an adaptation is seen in the dog; the horse or antelope shows an extreme development. The originally flexible skeleton becomes adapted almost entirely to a fore-and-aft motion of the legs, so that other motions become awkward or impossible. The foot, which originally lay nearly flat on the surface, in a semiplantigrade (palm-walking) position, tends to be lifted from the ground; and the metacarpals and metatarsals elongate, forming an extra limb segment (as in the hind legs of some dinosaurs and birds); the divergent hallux and pollex tend to be reduced and disappear. The animal now walks on the toes (digitigrade). The clavicle disappears, thus freeing the shoulder from any bony connection with the body and breaking the jar of landing on the front feet after a bound.

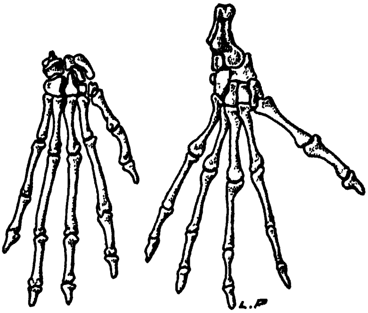


FIG. 248.—Manus and pes of *Notharctus*, an Eocene lemur. (After Gregory.)

The dog has reached a stage such as that outlined above. But many forms have progressed beyond this, with the development of hoofs and further reduction of toes, to the ungulate (hoofed) condition to be considered in a later chapter; while heavy ungulates have, in relation to the carriage of weight, developed ponderous, straight legs analogous to those of the sauropod dinosaurs—these are the graviportal (weight-bearing) types.

Still other types which have progressed considerably toward fast locomotion on the ground are leaping forms, as the kangaroos and jumping rats, in which the body is held partially or fully erect and the propulsive force is a sudden spring with the hind legs.

In a number of groups, especially among primitive placental insect-eaters, underground burrowing types have developed in which the most prominent adaptation is the development of very strong front legs for digging purposes.

In tree-living forms the skeleton remains flexible in correlation with the necessity for agility. Adaptations are present for holding onto the trees, often by an opposable thumb and big toe but sometimes merely through sharp claws for digging into the bark. The tail is usually well developed as a balancing organ and is often prehensile. Some forms tend to swing more especially by the hands (brachiation), with interesting evolutionary results. These adaptations are discussed in detail in connection with the primates. A further tendency on the part of tree-living types has led in a number of groups to the development of gliding forms, in which a membrane has developed in connection with the limbs; and a final stage in this evolutionary process has resulted in the development of true flight in the bats.

Again (as in reptiles) mammals may tend to revert to an aquatic existence. A number of marine mammals, such as seals, whales, sea cows, sea otters, have developed. The limbs are retransformed into finlike organs; the fusiform body shape of the fish tends to be reassumed; a tail fin, and even a dorsal fin, may be redeveloped.

CHAPTER 16

PRIMITIVE MAMMALS

LIVING mammals are easily divisible into (1) monotremes (the duckbill and spiny anteaters of Australia), which are egg-laying types; (2) marsupials, including the opossums and a large number of Australian forms which bear the young alive but at an immature stage; (3) placentals, in which the young are retained longer within the mother's body and a highly developed placenta is present. The first are called the subclass Prototheria, or primitive mammals; the second and third together may be termed the Theria, or true mammals, with the term Metatheria applied to the marsupials and Eutheria to the placentals. Such divisions are satisfactory for living forms. But the monotremes are almost unknown as fossils, and marsupials and rare placentals appear only at the end of the Cretaceous. Most Mesozoic fossil forms pertain to orders not particularly close to living groups; and, since we have no knowledge of their mode of reproduction, they are difficult to classify.

The mammal-like reptiles which flourished in Permian and early Triassic times had become very rare by the end of the latter period, and only a few specialized forms persisted into the Jurassic. Mammals presumably came into existence during the Triassic, but we know extremely little about their history during almost the entire span of the Mesozoic. As was noted earlier, there are few, if any, Triassic fossils which can be surely classed as mammals. In the Jurassic, mammals are definitely present; but almost all known remains come from two English localities and one small bone pocket at Como Bluff, Wyoming. Between the Upper Jurassic and the Upper Cretaceous, when marsupials and the first placentals appear, we know but two or three teeth. Further, almost all the earlier Mesozoic remains consist of isolated teeth or, at the most, jaws; prior to the Upper Cretaceous we have not one single skeleton, not one complete skull. Even in the Upper Cretaceous, mammal remains are rare, mostly fragmentary, and are found only in a few areas in North America and Mongolia. In consequence, we are as yet in the dark as to much of the history of Mesozoic mammals. We know little except the dental anatomy of the forms which have been found; and the sparseness of the record suggests that many groups may well have existed but have escaped discovery.

This absence of material is, presumably, not due to any great rarity of mammalian life during these times but to the small size of the Mesozoic mammals. On the average they were no bigger than a rat or a mouse; and the delicate bones of such forms would seldom be preserved and, even if exposed, would tend to be overlooked by collectors.

Monotremes.—Before considering these early fossil types, it will be advisable to discuss the living members of the order Monotremata, a group which is paleontologically almost entirely unknown but which must have had a long independent history. The duckbill (*Ornithorhynchus*) and spiny anteaters (*Echidna* or *Tachyglossus*, etc.) of Australia—the only living monotremes—are among the most bizarre and paradoxical of living vertebrates.

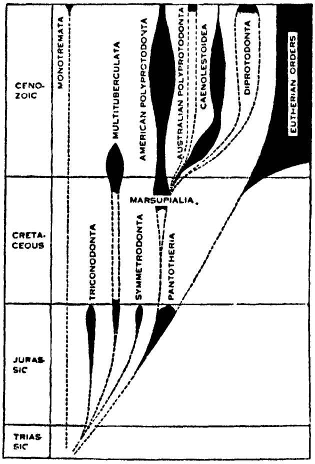


FIG. 249.—Chronologic distribution of the lower mammalian types

They have such mammalian features as milk glands (of primitive structure), hair, and but one lower-jaw element. However, they are exceedingly primitive in that, in contrast to all other mammals, they still lay eggs, while many other reptilian characters are present in their skeletons and soft anatomy. They are highly specialized in their modes of life and in consequent adaptations, such as the loss of teeth, development of a bill, and peculiar limb structure for digging or swimming. The spiny anteater has a pouch like that of marsupials.

The duckbill has a broad bill; the anteater, a long slim beak suitable for ant-eating. Both are toothless as adults. The anteater has no trace of teeth; in the duckbill there are a few irregularly shaped molar rudiments in the young which have been compared (but with little success) to those of the fossil multituberculates. The braincase is moderately expanded; the frontal bones are unusually small, the nasals large. There is no lacrimal, and the jugal is reduced or absent. There is a large palatine forming part of the long secondary palate; the ectopterygoid (in contrast with other mammals) has been retained; there is a large vomer and an additional pair of small problematical bones at the front of the palate. The orbitosphenoid is large; pterygoid and alisphenoid are present but peculiarly developed. There is no formation of an auditory bulla; the tympanic bone is a loose open ring, and the recess for the middle ear is only partially inclosed by extensions from the petrosal and alisphenoid. The jaws are reduced.

The presence of unfused cervical ribs is again a primitive feature. The shoulder girdle (Fig. 222, *C*) is emphatically reptilian; for an interclavicle is still present, there are two large ventral coracoid elements, and in the scapula there is no spine or supraspinous area. In the pelvis (Fig. 223, *D*) there are long marsupial bones extending forward from the front of the pubis, as in marsupials. The limbs are highly specialized for digging.

There are remains of both monotreme types in the Pleistocene of Australia; beyond this we know nothing about the history of this group; the absence of teeth, coupled with other marked specializations in the living monotremes, renders comparison almost impossible. Certainly, they are very primitive, as well as highly specialized; and it has been suggested that they represent a line of descent from mammal-like reptiles entirely separate from that of other living forms. Their survival in the Australian region may be attributed partly to their specialized mode of life and partly to the long isolation of that region from other continents.

Jurassic mammals.—The four orders next to be considered constitute the entire mammalian fauna of the few localities in Europe and North America in which Jurassic mammals are present; except for the aberrant multituberculates, these groups are unknown in later periods. They are by far the oldest of known mammals, barring the problematical Triassic types mentioned in our discussion of advanced therapsids. Osteological evidence suggests that they were well above the evolutionary level of the egg-laying monotremes and thus properly to be classed with the marsupials and true placentals among the Theria. They include, presumably, the ancestors of these later groups and are thus of great phylogenetic importance. All, however, were of modest size, and, in consequence, their remains are rare and consist mainly of isolated teeth, occasional jaws, and a few limb bones and skull fragments.

Triconodonts.—The order Triconodonta comprises a series of forms from both Middle and Upper Jurassic which grew to relatively large size; *Triconodon* of the Upper Jurassic was the size of a cat. Very probably they were true carnivores, rather than insectivorous types. The dental formula reached as high as 4·1·4·5 for the lower jaw; incisors, large canines, relatively simple premolars, and molars were differentiated in typical mammalian fashion. The molars in such forms as *Triconodon* or *Priacodon* (Figs. 250, *A;* 251) had three sharp conical cusps of about equal height, arranged in a fore-and-aft row, upper and lower cheek teeth meeting in a longitudinal shearing device. In *Amphilestes*, a more primitive member of the group, the middle cusp was the tallest, and the three were not so discrete; and it is obvious that these teeth might easily have been derived from a type such as that seen in *Cynognathus* and certain other therapsids. A natural cast shows the brain to have been very small and primitive. This group was once believed to demonstrate a stage in the development of the type of molars characteristic of higher mammals. But more probably the triconodonts were a divergent side branch not ancestral to other forms.

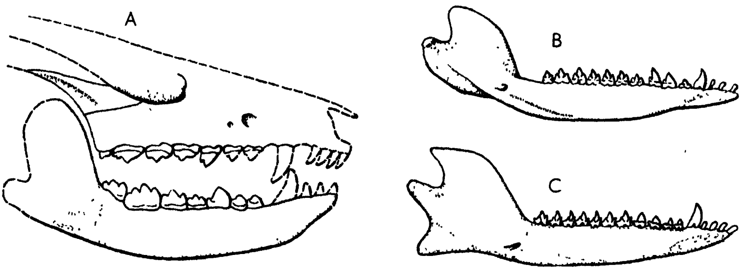


FIG. 250.—Jurassic mammals. *A*, Restoration of front part of skull of *Priacodon*, a triconodont, about twice natural size; *B*, inside of jaw of *Spalacotherium*, a symmetrodont, about 3/2 natural size; *C*, inside of jaw of *Amphitherium*, a pantothere, about twice natural size. (After Simpson.)

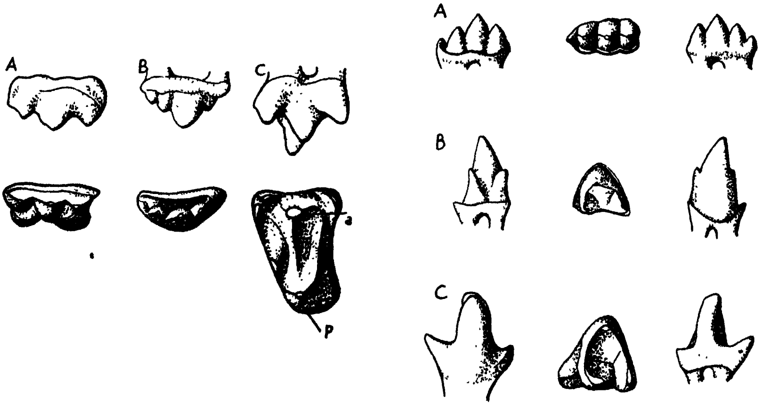


FIG. 251.—Molar teeth of Jurassic mammals. *Left*, right upper molars, external and crown views. *A*, *Priacodon*, a triconodont (×4½); *B*, *Eurylambda*, a symmetrodont (×6⅔); *C*, *Melanodon*, a pantothere (×7½). In *C*: *a*, amphicone; *p*, probable homologue of placental protocone. *Right*, lower left molars, internal, crown, and external views. *A*, *Priacodon*, a triconodont (×7/2 approx.); *B*, *Spalacotherium*, a symmetrodont (×5); *C*, *Dryolestes*, a pantothere (×11). (After Simpson.)

Symmetrodonts.—The order Symmetrodonta has been established for the inclusion of a number of late Jurassic forms, such as *Spalacotherium* (Figs. 250, *B;* 251, *B*) and *Eurylambda* (Fig. 251, *B*), also of comparatively good size and comparatively predaceous habits. These forms also had three separate cusps in each molar tooth and hence were at one time included in the triconodonts, with which group they agree in the absence of an angular process on the jaw. But in the present types the three cusps were arranged in a symmetrical triangle, with the base external above, internal beneath. Early advocates of the tritubercular theory believed that they had arisen from triconodonts by a rotation of the cusps. But there is no evidence of such rotation, and they probably had nothing to do with that group. Although possibly related to the next order, the symmetrodonts seem to have been somewhat off the main evolutionary line. The symmetry of the molar tooth in this group is in contrast to the molar shape of pantotheres, and the lower molars lack the "heel" characteristic of that order and of all later mammalian groups.

Pantotheres.—Most important of Jurassic orders from an evolutionary point of view is that of the Pantotheria, frequently termed Trituberculata (Figs. 250, *C;* 251, *C;* 252). Most representatives are from the late Jurassic; *Amphitherium*, the only Middle Jurassic genus, is a generalized form but known only from the lower jaw. In *Amphitherium* this is long and slender, and, in contrast to other Jurassic orders, there is a well-developed angular process. In addition to four incisors, a canine, and four premolars, there are seven molar teeth—an unusually high number but perhaps a rather primitive one. The molars show a three-cusped, asymmetrical trigonid, comparable to that of later groups; and particularly significant is the presence of a "heel" or "talonid," absent in the orders so far mentioned.

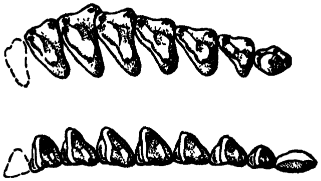


FIG. 252.—Reconstruction of the right upper and left lower rows of cheek teeth of a Jurassic pantothere. (After Gregory and Simpson.)

In the late Jurassic mammal localities of Europe and America, pantotheres are abundant and so varied that they are placed in three distinct families. The Paurodontidae, as the name suggests, have a much reduced tooth count; the Docodontidae are obviously specialized in molar structure; the Dryolestidae, such as *Melanodon*, appear to be closest to the generalized and primitive pattern. The lower molars in the last family are rather similar to those of *Amphitherium*. The upper ones are (as in early marsupials and placentals) asymmetrical triangular structures. At the internal apex there is a prominent cone which fits into the basin of the talonid, as does the placental protocone. More laterally there is a second prominent cusp, termed the amphicone; this may well be homologous with the paracone plus metacone of later orders.

The outer edge of the tooth has prominent marginal cusps or cingula, as in opossums and early insectivores.

Like the other Jurassic orders so far described, pantotheres are unknown in later strata (there are almost no remains of mammals in the Lower Cretaceous). But while our evidence is incomplete, it can at least be safely said that the known characters of the pantotheres allow us to consider them as possible ancestors for all higher mammalian types.

Multituberculates.—A specialized but highly successful and long-lived side branch of the early mammalian stock is that of the order Multituberculata. These forms appear to have been the first of herbivorous mammals, with skull and tooth specializations for the treatment of vegetable food somewhat analogous to those seen among the later rodents. In dental development they are closely comparable to some of the later marsupial types and to *Tritylodon* and its allies, discussed earlier. The multituberculates tended to grow (as do herbivores generally) to relatively large size. Contrasting with the diminutive size of most other Mesozoic mammals, some forms were as large as woodchucks; and multituberculates may have been not so far from that type of animal in superficial appearance and habits. The history of the group is a long one. They appear in the late Jurassic and, unlike contemporary orders, survived beyond the end of the Mesozoic to the base of the true Eocene before being wiped out, presumably by the competition of advanced placentals.

The skull was a massive one, broad posteriorly and roughly triangular in outline dorsally, although the snout, capped by very large nasal elements, is blunt and stoutly built. The great width across the arches indicates the presence of powerful jaw muscles. A curious feature of the zygomatic arches is the total loss of the jugals. In some forms (such as *Ptilodus* [Fig. 253]) there are large vacuities in the palate, both anteriorly and posteriorly. The basicranial region is very broad and flat and with structural details unlike those of any other mammalian order. A braincast shows the olfactory bulbs (and hence presumably the sense of smell) to have been developed to a remarkable degree. The heavy jaw resembles that of triconodonts in lacking an angular process.

The dentition is of a very specialized type. Anteriorly a pair of large incisors was developed above and below; smaller lateral incisors may persist in the upper jaw. Following a diastema (with loss of canines), there is a well-developed series of cheek teeth. The molars are the diagnostic multituberculate feature. The lower molars are elongated, with two parallel rows of cusps; the upper molars opposed them primitively with two, later with three, similar cusp rows, the whole forming an excellent masticatory device. The premolars were rather variable in nature and were frequently reduced. In the lower jaw most multituberculates have tended to enlarge the posterior premolar into a large, high, striated cutting tooth.

The postcranial skeleton, as far as known, is typically mammalian, without any of the reptilian traits seen in the monotremes.

The first multituberculates appear in the late Jurassic of Europe and North America and include such genera as *Ctenacodon* and *Plagiaulax*. As far as known, they had already developed all the essential features of multituberculate structure. These forms, however, were relatively small, had but two rows of cusps in the upper molars, and retained small lateral upper incisors. The order was a flourishing one in the late Cretaceous and Paleocene. *Cimolomys* and *Ptilodus* were representatives of the family Ptilodontidae in which there was a tendency to add a third row of cusps to the more elongate upper molars and to reduce the number of premolars. A very specialized group is that represented by *Taeniolabis* (Fig. 253) and several other Paleocene genera. *Taeniolabis* was a giant of the tribe (relatively speaking), with a broad, blunt skull half a foot long, very heavy incisors, premolars reduced almost to the vanishing-point, and large stout molars.

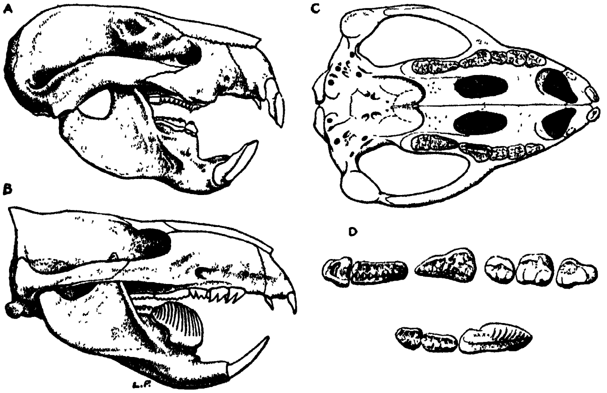


FIG. 253.—Multituberculates. *A*, Skull of *Taeniolabis*, original about 6¾ inches long; *B*, side view of *Ptilodus* skull, original about 3 inches long; *C*, palatal view of the same; *D*, upper and lower cheek teeth of *Ptilodus*, about twice natural size. (Mainly after Simpson.)

The multituberculates certainly were a sterile side branch of the early mammals; they are not ancestral to any later order, although certain marsupials paralleled them in dental development. Their ancestry is unknown. Their dentition, we have noted, presents similarities to that of *Tritylodon* and its allies, once thought on this account to be multituberculates; but the two types are dissimilar in all other known features. Monotreme relationships have been suggested; but the multituberculates are more advanced in the postcranial skeleton and show no skull resemblances. The dentition may have been derived from such a type as that seen in the still earlier triconodonts, by a doubling-up of an anteroposterior row of molar cusps, but there is no positive evidence of phylogenetic connection.

The early evolution of mammals.—Leaving aside the specialized multituberculates, remains of Jurassic mammals, although fragmentary, give us some idea of the primitive and early ancestors of the mammals of later ages. They were generally small creatures, averaging about the size of rats and mice, and were perhaps somewhat like these forms in their general appearance. Their food must have consisted mainly of insects; they were potential carnivores, but their size limited them to small prey. Other materials, however, such as birds, fruit, and eggs, may have made up part of their diet. The general degree of evolution of the known skeletal parts suggests that they were above the monotreme level of organization and that, therefore, they already nursed their young and presumably bore them alive, although at a relatively early stage in development. Their brains, as far as can be told, were still poor and small by modern mammalian standards, although much better than those of their reptilian ancestors. Presumably they were retiring in habits, possibly nocturnal, and to some extent arboreal. Inconspicuous and small they had to remain, for, as contemporaries of the dinosaurs, the threat of death from the great carnivorous reptiles lay constantly over them.

But this long period of "trial and tribulation" was perhaps not altogether disadvantageous. It was, it would seem, a period of training during which mammalian characteristics were being perfected, wits sharpened, developmental processes improved, and the whole organization undergoing a gradual evolutionary change from reptilian to true mammalian character. As a result, when (at the close of the Cretaceous) the great reptiles finally died out and the world was left bare for newer types of life, the mammals had evolved into a group prepared to take the leading place in the evolutionary drama.

Marsupials.—In the late Cretaceous beds we find that, although the multituberculates still flourished, the three typical Jurassic orders had disappeared. The triconodonts and symmetrodonts seem to have left no descendants; but, seemingly developed from the pantothere stock, we find representatives of the two great living groups of mammals—the marsupials and the placentals. The representatives of both groups were still small insectivorous types and again are poorly known. The placentals, which were to dominate the scene in the Cenozoic, were rare. Much more abundant were small opossum-like forms—the earlier marsupials, or pouched mammals.

Today the marsupials constitute a well-defined group including the opossums and a few other New World mammals, together with a large array of types constituting the greater part of the fauna of the Australian region. Certain of their distinctive features are suggested by the name. Almost all have a pouch placed on the belly of the female, which contains the teats and in which the young are carried after birth. This marsupium is rendered necessary because of the fact that birth takes place at a very small and immature stage, and this, in turn, is due to the fact that an efficient placenta has been evolved in but a few members of the group. Among the definite osteological characters that separate them from the monotremes is the fact that (as in higher types) the coracoids are reduced to a single nubbin of bone on the under side of the scapula, a spine is developed on the latter bone, and the interclavicle is lost. Among the more prominent key characters which separate all known forms from higher, placental mammals are the inflected (or inturned) angular process of the jaw (Fig. 254, *F*), the usual presence of four molars and but three premolars, and the presence of a pair of marsupial bones articulating with the front of the pubes as in the monotremes (Fig. 223, *E*).

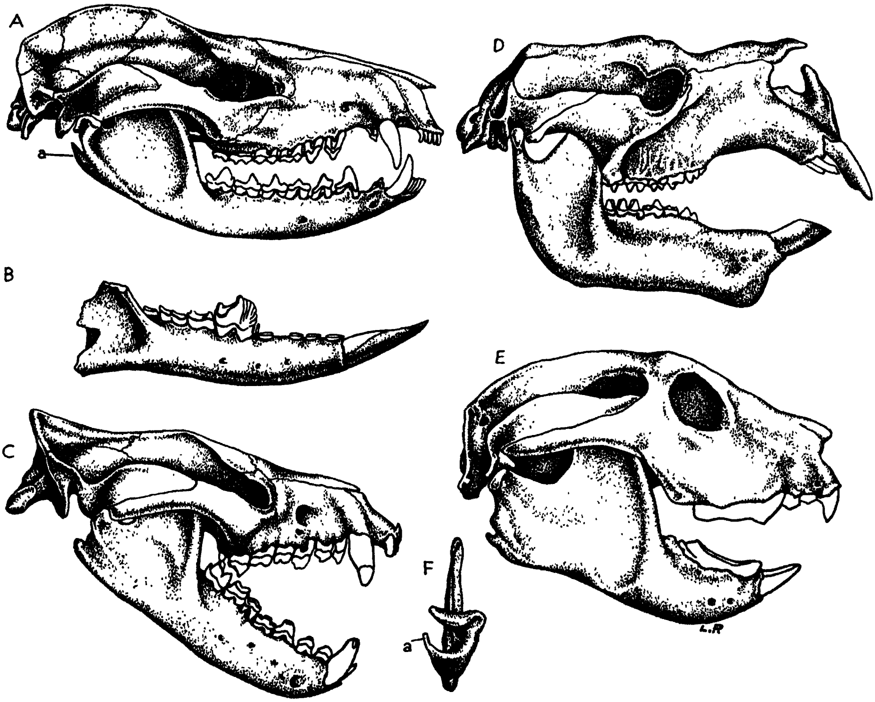


Fig. 254.—Skulls of marsupials. *A*, The living opossum, *Didelphis*; *B*, jaw of *Abderites*, a Miocene South American caenolestid (×½); *C*, *Borhyaena*, a South American Miocene carnivore, skull length about 9 inches; *D*, *Diprotodon*, a giant Australian Pleistocene diprotodont, skull length about 40 inches; *E*, *Thylacoleo*, a large Australian Pleistocene type with highly developed shearing teeth, skull length about 1 foot; *F*, opossum jaw (*right*) from the rear to show inflected angle (*a*). (*B* after Ameghino and Simpson; C after Sinclair; *D* after Owen; *E* after Owen and Anderson.)

In such a marsupial as the opossum, the brain is very small and the braincase region of the skull (Fig. 254, *A*) is consequently small compared with that of the average placental; sagittal and transverse crests are, in consequence, usually prominent. There is never any development of a postorbital bar behind the small orbits. There is never a well-formed auditory bulla of placental type, although the alisphenoid usually sends back a process to protect the middle ear.

In the oldest-known marsupials there appear to have been as many as five upper incisors, as is still the case in the opossum; there are seldom more than the conventional three in the lower jaw. Large canines were undoubtedly present in the ancestral forms as they are today in many of the more primitive carnivorous types. In the cheek series there are never more than three premolars and usually four molars. The problem, however, is complicated by the fact that there is almost no tooth replacement, the last premolar being the only one with a predecessor; the more anterior teeth are seemingly permanent milk teeth.

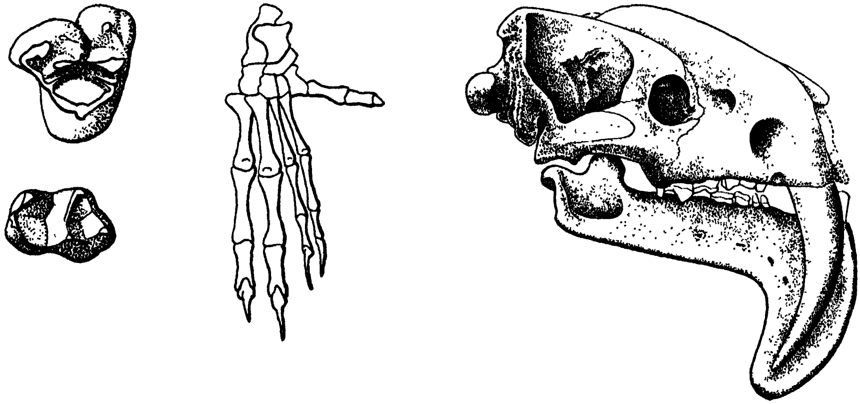


FIG. 255.—*Left,* upper right and lower left molar teeth of an Upper Cretaceous opossum. In the upper molars there is a well-developed row of outer cusps in addition to the normal trigon. (Much enlarged; after Osborn.) *Center,* foot of a living diprotodont marsupial to show syndactylous structure. *Right,* the skull of *Thylacosmilus,* a Pliocene South American carnivorous marsupial comparable to the placental saber-tooths; about ½ natural size. (After Riggs.)

In the more generalized forms (Fig. 255) the teeth are tribosphenic, with triangular upper molars and a trigonid and talonid below. In the upper molars there is developed a trigon similar to that of placentals but, in addition, an outer row of unnamed cusps which is presumably a primitive feature. In herbivores the teeth tend to square up with more or less development of a grinding surface.

A clavicle is almost always present in marsupials. There is seldom any reduction of toes in the front foot. In the hind foot the hallux appears to have been primitively opposable. There is often (especially in herbivorous types) a curious sort of syndactyly (Fig. 255) in which the fourth toe is strong and elongated and the second and third toes are united and balance the fifth toe, while the first digit may be lost. Claws are always present. It has been suggested that the primitive marsupials were arboreal, and many of the structural features tend to bear this out.

The customary division of the order Marsupialia is into the suborders Polyprotodonta and Diprotodonta; and this type of classification may well be retained, although parallelism in evolution makes it difficult to give a clear-cut distinction. The first group, of which the oppossum is typical, is the more primitive, including insectivorous, omnivorous, and carnivorous forms. The diprotodonts are mainly living Australian herbivores.

American polyprotodonts.—A primitive feature of the polyprotodonts (as the name implies) is the retention of an unreduced and unspecialized set of incisors; there may be as many as five in the upper jaw. The molars are generally triangular in shape and usually sharp cusped; there is usually no syndactyly in the foot. There are several families, among which the Didelphidae are the stem group.

Opossums (*Didelphis*, etc. [Figs. 254, *A;* 255]) and their relatives, found today in both western continents, are in almost every respect ideal ancestors for the whole marsupial group. There are five upper incisors and four lower ones; the upper molars are triangular in shape and rather sharp cusped (the diet is omnivorous, with a tendency toward the carnivorous side). The tail is usually prehensile; the limbs are of normal construction without any reduction of toes and with a well-developed, clawless, opposable hallux used for grasping in the opossum's arboreal mode of locomotion. In the late Cretaceous of North America are found forms very similar to the living opossums, and in the early Tertiary these forms are known from both Americas and from Europe as well; but since the Miocene they seem to have been confined to the Western Hemisphere. The opossums have lived continuously in South America since then; but in North America there are no fossils of this group in the late Tertiary, and we cannot be sure whether or not our living opossum is really an oldest inhabitant or whether he is a recent reimmigrant from the south.

South America seems to have been separated from the other continents at the beginning of the Eocene. Marsupials were evidently present there at the time, and in addition some placental mammals. But no placental carnivores appear to have gained admission, and thus there came about a good opportunity for the development of purely carnivorous marsupial types. These South American carnivores are separated as a distinct family, the Borhyaenidae. They were terrestrial forms, rather short-legged, with large skulls. The claws were strong and compressed; and the hallux, as in running types generally, was reduced. The teeth, as in true carnivores, tended to the shearing type. These carnivores ranged in size from that of the opossum to that of a bear and were especially abundant in the Miocene, where *Prothylacinus* (Fig. 256) and *Borhyaena* (Fig. 254, *C*), a puma-like form, were typical. Following that period, however, there arrived higher ungulate types, displacing these beasts' former prey, and placental carnivores, displacing these marsupials, which soon became extinct. A curious last survivor in the Pliocene was *Thylacosmilus* (Fig. 255), with large stabbing tusks like those of the saber-toothed tiger.

Somewhat similar forms are found today in Australia. The presence of these carnivores in South America has been used by some as an argument for a direct connection between these continents. But it appears more probable that this is a case of parallel development from the late Cretaceous marsupial stock in two isolated regions.

Australian polyprotodonts.—It is generally believed that Australia became separated from the rest of the world in late Cretaceous days, at so early a time in mammalian evolution that no placentals of any sort gained admission; and, except for bats and some rodents, few or none have entered since except those brought in by man. We know almost nothing of the Tertiary fossil history of Australia, but it seems reasonable to assume that the earliest mammalian fauna was composed of primitive opossum-like marsupials, from which have descended the varied living marsupial groups which constitute the great bulk of the Pleistocene and Recent mammals of that continent. The most direct descendants of the primitive settlers appear to be carnivorous types which are called "native cats," or (incorrectly) "opossums" (*Dasyurus*), and a number of mouselike, insect-eating forms. Somewhat more advanced is the Tasmanian devil (*Sarcophilus*), a powerful carnivore with shearing molars, while a most specialized type is the Tasmanian "wolf" (*Thylacinus*), a very wolf-like animal similar to some of the South American Miocene marsupials. There are some interesting side branches included in this group, such as a marsupial anteater—with typical ant-eating adaptations in the long snout, reduced teeth, and long claws—and a marsupial molelike type. There are, in addition, some Australian Pleistocene and

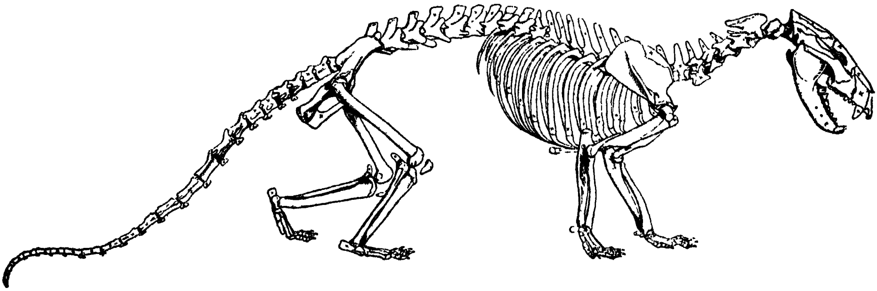


FIG. 256.—*Prothylacinus*, a Miocene carnivorous marsupial from South America, about 4 feet long. (From Sinclair.)

Recent forms which have diverged farther from the common polyprotodont stock—the bandicoots, such as *Perameles.* These are insectivorous to omnivorous in diet, rabbit-like in size and in appearance except for the long pointed snout. The molars tend to become grinding teeth and assume a square shape with blunter cusps. The hind legs are long, the feet slim with some tendency toward syndactyly and with an emphasis on the fourth toe, very much as in the kangaroos.

Diprotodonts.—A second prominent group of marsupials is that of the Diprotodonta, confined to Australia and almost entirely unknown before the Pleistocene, in which period most of the existing types were represented. Despite our lack of knowledge of earlier fossils from Australia, it is obvious that they are a herbivorous development from the primitive opossum stock. However, many structural changes have occurred. There are never more than three upper incisors, and often there is a development of chisel-like teeth similar to those of rodents. The molars are quadrate in shape. The hind foot is generally syndactylous.

In the great majority of diprotodonts three upper incisors are still present. Seemingly closest to the common ancestors are the phalangers (*Phalanger,* etc.)—arboreal types, the marsupial "squirrels," including even flying "squirrels." Somewhat more advanced is *Potorous* [*Hypsiprymnodon*], the musk "kangaroo," in which, as in kangaroos, the last premolar is a long, straight-edged cutting tooth similar to that of the multituberculates; the limbs, however, are primitive in structure. The true kangaroos (*Macropus,* etc.) have gone further in the development of long hind legs for hopping, with a reduction of the lateral toes and emphasis on the fourth.

Two interesting living forms are characterized by the fact that in the upper jaw, as well as in the lower, there is a large pair of chisel-like teeth, the other upper incisors being small to absent. The living types include: *Phascolarctos,* an arboreal form rather like a large Teddy bear in size and appearance; and *Phascolomys,* the wombat, rather like the woodchuck in habits. Both have large Pleistocene relatives, and in addition there are a number of large extinct Pleistocene marsupials from Australia with a diprotodont dentition. *Diprotodon* (Fig. 254, *D*) is the largest-known marsupial and was a form about the size of a large rhinoceros but with a lumbering build suggesting similarity to the living wombat. *Thylacoleo* (Fig. 254, *E*) was even more odd, a form the size of a lion with reduced molars and with the last premolars developed into large shearing teeth. It has been argued that *Thylacoleo* was a carnivore, but it seems more likely that it was really a diprotodont and that the shearing teeth were used in cutting fruit.

Caenolestoids.—The two suborders discussed above are the standard divisions of the marsupials and have been recognized for nearly a century. But certain living and fossil South American forms do not seem to fit in well with either group; and for their reception the creation of a third suborder, the Caenolestoidea, is necessary. *Caenolestes* is a small, living, South American form, mouselike in size and appearance (and long thought to be a rodent). There are four upper incisors, and the feet are not syndactylous, so that it should be a polyprotodont. But although there are three or four lower incisors, the middle ones are elongate as in diprotodonts, the molars are quadrate, and the last lower premolar in some related fossil genera is a cutting type like that of kangaroos. This group goes back in South America to the Eocene. Some of the earlier forms, such as *Polydolops* and *Abderites* (Fig. 254, *B*) went far in diprotodont specializations, for there was but a single upper and lower incisor, as in the more advanced Australian forms. The upper molars were rather like those of multituberculates, and some writers have tended to group them together, but this is merely convergent evolution. Presumably in the radiation of the marsupials in the late Cretaceous or Paleocene, primitive types which were still polyprotodonts migrated both to Australia and to South America. In the former continent some developed into the true diprotodonts. The caenolestoids with the same ancestry, and presumably the same evolutionary tendencies, paralleled them closely and also paralleled the earlier mammalian herbivores, the multituberculates.

Marsupial history.—It is reasonable to think that the marsupials are derived from the pantotheres, although there is no evidence that those Jurassic forms had certain of the peculiarities of the true marsupials. It has often been assumed that the marsupials are the ancestors of the placentals. That the ancestors of the placentals passed through a stage in which the young were born immature, as in marsupials, is theoretically probable; but that these ancestors were marsupials in the sense in which we know them (with a pouch, marsupial bones, and inflected jaw angle) is quite doubtful. Indeed, we now know primitive placentals fully as old as the earliest opossum-like forms. It is probable that placentals have descended directly and independently from the pantotheres and that the marsupials are a parallel branch of the mammalian stock.

But, while not on the direct line of descent, the more primitive marsupials (such as the opossums and some of the smaller dasyurids) in their mode of life, in their insectivorous-omnivorous diet, and in many structural features give us a good picture of the Mesozoic forms from which the Tertiary mammals have come. It is of interest to note that the opossums and primitive diprotodonts are primitively arboreal types, in agreement with the suggestion that the ancestral mammals were tree-living forms.

It is probable that primitive marsupials had a world-wide distribution in the late Cretaceous. But early in the Tertiary they became almost entirely restricted to two regions—South America and Australia—presumably because they were unable to compete successfully with more highly developed placentals. In South America late Tertiary placental invasions caused the extinction of many types, and only *Caenolestes* and the opossums have survived. But in Australia the marsupials in the absence of competition radiated out into many different modes of life. A number of forms are still arboreal, but the great majority have become ground dwellers of many sorts. From the primitive omnivorous-insectivorous diet the living marsupials have branched out into purely carnivorous and herbivorous modes of life. In Australia the marsupials, given their chance for development, have paralleled almost every type which the placentals have produced on the other continents.

CHAPTER 17

PLACENTAL ORIGINS; INSECTIVORES; BATS

EXCEPT for the primitive and aberrant monotremes and the marsupials just considered, all living mammals are members of a single more advanced group which has been dominant since the beginning of Tertiary times—the Eutheria, commonly termed placental mammals. In these mammals we find a well-developed placenta formed from the allantois, one of the embryonic membranes; this permits of a long period of prenatal development and of birth at a more advanced stage than was possible in marsupials. The popular name is somewhat misleading, for some of the living marsupials have paralleled the true placentals to a considerable extent in the development of this structure; but there are many other points of difference between the two groups. There is no pouch in placentals, marsupial bones are absent, there is almost never the inflected angle of the jaw characteristic of marsupials, the brain becomes considerably advanced over that of the more primitive types, the dental formula was originally $\frac{3\cdot1\cdot4\cdot3}{3\cdot1\cdot4\cdot3}$ and almost never exceeds that number, and there is typically one complete replacement of all the teeth except the molars.

Primitive placental structure.—From what we know of living and fossil types it is possible to picture a typical primitive placental at the end of the age of reptiles. Such a type would have been small in size, as had been the ancestral trituberculates of the Jurassic, and the limbs short. The clawed feet would have been applied rather fully to the ground in a semiplantigrade position, and there presumably would have been a somewhat opposable pollex and hallux. Among technical diagnostic characters in the limbs would have been the presence of a clavicle, a central bone in the wrist, an entepicondylar foramen in the humerus, and a third trochanter on the back of the femur—all characters lost in many later placentals. There would have been about twenty thoracic and lumbar vertebrae between neck and pelvis.

The brain was presumably comparatively small and poorly organized—that is, with the olfactory lobes and olfactory bulbs large and unreduced and with the neopallium but little developed. The skull, however, would have been fairly large (in correlation with the smallness of the beast), with a long facial region and large eyes, and there would have been no development of a postorbital bar. The dentition would have contained the primitive placental number of teeth and in general appearance would have resembled that of the older pantotheres. The lower molars would have been tribosphenic in character, with trigonid and talonid; the upper molars, triangular, with an internal protocone and, somewhat in from their outer edges, not the amphicone present in the older types but two cusps, the paracone and the metacone, derived from the division of the primary reptilian cone.

Quite probably these forms were inconspicuous forest dwellers and nocturnal to some degree at least. Certain characters in their descendants (such as the frequently divergent pollex and hallux) suggest an early arboreal habitat, although in most placental types terrestrial life seems to have been taken up at an early date. The diet presumably still consisted essentially of insects but was varied with other types of soft plant and animal food, such as fruits, worms, and grubs.

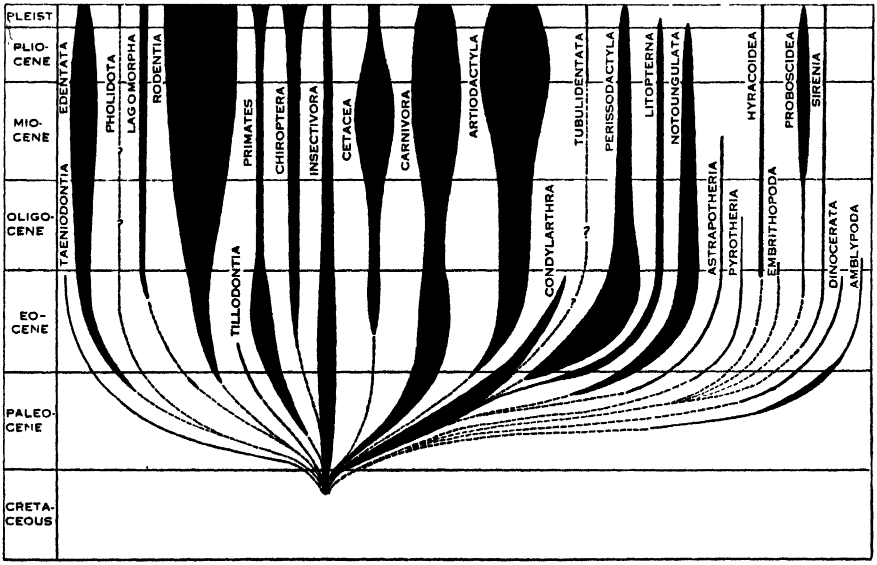


FIG. 257.—The chronologic distribution of the placental mammals

Such a form as that described above was a purely hypothetical creature two decades ago, for pre-Cenozoic placentals were unknown. Now, however, we possess a few skulls from the Upper Cretaceous of Mongolia which are definitely placental in nature.

Small and seemingly rare as the earliest placentals were, they were nonetheless the most efficiently organized land dwellers of the times, better in brains and in mode of development than the marsupials and multituberculates that were their mammalian contemporaries. With the disappearance of the dinosaurs, their spread was rapid. At the beginning of the true Eocene the multituberculates made their last appearance, marsupials had become rare in the Northern Hemisphere, and the placentals had already become differentiated into the ancestors of almost all the known orders of later Tertiary and Recent times.

Insectivores.—As was the case with their Jurassic ancestors, the early placentals were presumably insectivorous in diet. There are still in existence today a number of mammals, such as the shrews, moles, and hedgehogs, which have retained similar feeding habits and which have, despite various specializations, many primitive characters. These forms, grouped with related fossil types as the order Insectivora, are regarded as the most direct descendants of the primitive placentals.

The insectivores are not and probably never have been an abundant group; today they are small in size and few in number. Most of them are highly specialized or are isolated island forms, as is usually the case with surviving members of primitive groups.

Since they include the supposed stem of the later placental types, insectivores can be characterized for the most part only negatively as lacking the specializations of other derived forms. Many common features were noted above as characteristic of a generalized ancestral placental. The tympanic cavity is usually an open hole, partially surrounded by processes from neighboring bones, with the tympanic bone an open ring. In many instances the zygomatic arch is incomplete. The teeth are almost always sharp-cusped, and in a majority of cases there is but little departure from primitive placental types of dentition. The incisors are somewhat variable in development, and the canines are often somewhat reduced. There is usually little modification or reduction in the limbs except in burrowers.

It is obvious that several different types of animals may be, and are, placed in the order Insectivora. Three major categories may be distinguished: A, the primitive placentals and modern "relics" of this primitive stage; B, typical insectivores of more modern types; and C, several mammalian groups which have diverged from the primitive placental pattern but are still fairly close to the insectivore type and are not important enough to merit the erection of separate orders for their reception. Group A we shall term the suborder Zalambdodonta, including the superfamilies Deltatheridioidea (primitive), Centetoidea, and Chrysochloroidea (surviving primitive relics). The typical insectivores (Group B) are here termed the suborder Dilambdodonta, including the superfamilies Erinaceoidea, Soricoidea, Pantolestoidea, and Macroscelidoidea. In Group C we shall list as suborders the extinct Mixodectoida and the living Dermoptera.

Primitive insectivores.—Of the placental types known from the Cretaceous of Mongolia, some are typical, although quite primitive, insectivores of the hedgehog group. Another series of forms, however, includes several small mammals, such as *Deltatheridium* (Figs. 258; 259, *A;* 260, *A*), which appear to be not far removed from the base of the entire placental stock. The skull of *Deltatheridium* was of a very generalized type; and there were none of the specializations, such as the elongated snout, weak zygomatic arch, or peculiar incisor development, found in later insectivores. Particularly interesting was the development of the upper molars. The paracone and metacone were situated almost in the center of the tooth, and the two cusps were only barely separated at their tips. This is a condition seemingly intermediate between that found in the Jurassic pantotheres, in which the homologue of paracone and metacone appears to be the single, centrally situated amphicone, and that found in typical placentals, in which paracone and metacone are widely separated and placed close to the outer margin. Somewhat similar molars are found in some of the carnivorous placentals and certain later insectivores discussed below. It may be that *Deltatheridium* was on the line leading to one or the other of these later groups, but it was certainly exceedingly close to our ideal of an ancestor for the entire placental stock. Forms closely related to *Deltatheridium* are found, although rarely, in North American Paleocene and Eocene beds.

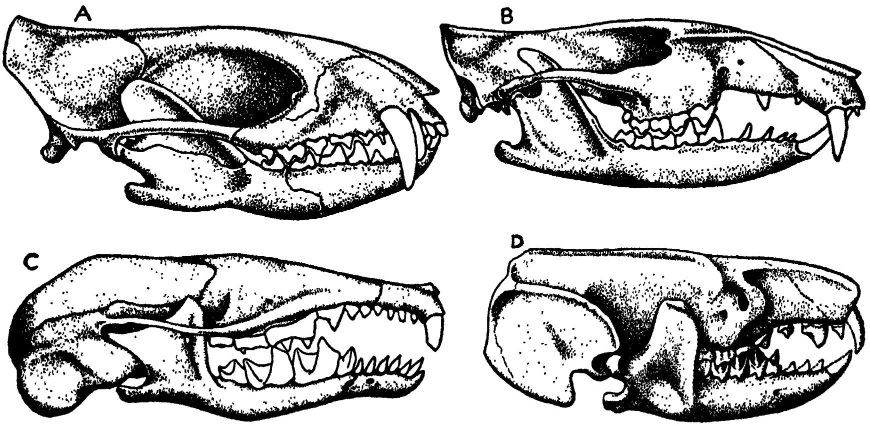


FIG. 258.—Skulls of insectivores. *A*, *Deltatheridium*, a primitive Cretaceous form from Mongolia, skull length about 1¾ inches; *B*, *Zalambdalestes*, a Cretaceous erinaceoid, skull length about 2 inches; *C*, *Proscalops*, an Oligocene and Miocene soricoid, skull length about 1 inch; *D*, *Apternodus*, an Oligocene zalambdodont, skull length about 1¾ inches. (*A*, *B* after Gregory and Simpson; *C* after Matthew; *D* after Schlaikjer and Scott.)

Modern zalambdodonts.—Highly specialized in many respects, but primitive or even regressive in their molar structure, is a series of curious living insectivores frequently termed the Zalambdodonta. They appear to be fairly direct descendants of the Cretaceous forms just considered, and we here include them in the same suborder. The greater number of the living types are often grouped in the family Centetidae, found on the isolated island of Madagascar. The smaller members of the group tend to parallel the shrews, moles, and hedgehogs of other regions in their adaptations; the largest form, *Centetes*, the tenrec, is the giant among insectivores, its tailless body measuring about 20 inches in length. Closely related to the centetids is *Potamogale*, the otter shrew, a good-sized form from West Africa, which is a fish-eater with a strong tail for swimming. Another related form is *Solenodon* of Haiti and Cuba, a fairly large, long-snouted, rather ratlike insectivore. *Chrysochloris*, the golden mole of South Africa, which superficially resembles the ordinary moles in its adaptations, is another archaic insectivore type. It differs, however, very markedly in many anatomical features from other recent zalambdodonts and merits a place in a separate superfamily at least.

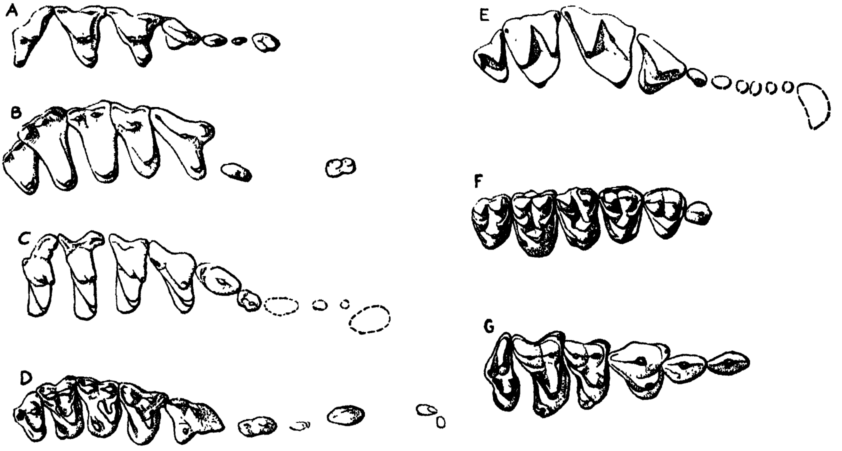


FIG. 259.—Right upper cheek teeth of insectivores. *A*, *Deltatheridium* (×2½); and *B*, *Zalambdalestes* (×3), primitive Cretaceous forms; *C*, *Palaeoryctes*, a Paleocene zalambdodont (×3); *D*, *Diacodon*, an Eocene erinaceoid (×5/4); *E*, *Proscalops*, an Oligocene and Miocene mole (×4 approx.); *F*, *Elpidophorus*, a Paleocene mixodectid (×3½ approx.); *G*, *Bessoecetor*, a Paleocene pantolestid (×3). (*A*, *B* after Gregory and Simpson; *C–E* after Matthew; *F*, *G* after Simpson.)

The abundance of living zalambdodonts in Madagascar as contrasted with their rarity elsewhere seems to be due to the isolation of that island from early Tertiary times on. (The lemurs, we shall see, offer a similar history.) There is little fossil material which can be assigned to the modern families. The centetids and golden moles are known from the Pleistocene; *Potamogale* is unknown in fossil form. There are, however, several American Oligocene genera, such as *Apternodus* (Fig. 258), and *Palaeoryctes* (Fig. 259, *C*) of the Paleocene, which appear to connect the living zalambdodonts with the primitive stock.

In the "modern" zalambdodonts the upper molars are triangular in shape. There is a low cone at the inner apex, accessory tubercles at the outer edge, and, nearly in the center, there is in most cases a high, V-shaped single cusp. This was originally thought to be the protocone; but it is now generally agreed that this represents the original single reptilian cusp, while the protocone is the lower internal structure. The tooth thus has a pattern rather resembling that of the pantotheres. This resemblance, however, is quite certainly not due to any direct descent from that Jurassic group. Some show the central cusp partially or completely divided and render it probable that these surviving families have passed through a stage represented by *Deltatheridium* and are regressive rather than truly primitive in structure.

Typical insectivores: erinaceoids.—Apart from their historical importance as placental ancestors, the Insectivora merit consideration in another role, if a more modest one—that of a specific, "modernized" placental group which, despite specialization, has successfully continued during the Cenozoic in the insectivorous mode of life of the Mesozoic ancestral mammals. The modernized insectivores are here considered to constitute a suborder, the Dilambdodonta, within which several superfamilies may be distinguished. In these modern groups the upper molars are not of the old-fashioned type described for the zalambdodonts; the paracone and the metacone are well separated. The eyes tend to be rather poorly developed, the zygomatic arch, if present, is feeble, and there is a long tubular snout region.

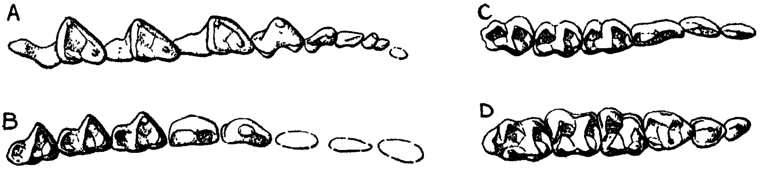


Fig. 260.—Left lower cheek teeth of insectivores. *A*, *Deltatheridium*, a primitive Cretaceous form (×2½); *B*, *Diacodon*, an Eocene erinaceoid (×5/4); *C*, *Elpidophorus*, a Paleocene mixodectid (×3½ approx.); *D*, *Bessoecetor*, a Paleocene pantolestid (×3). (*A* after Gregory and Simpson; *B* after Matthew; *C*, *D* after Simpson.)

The more primitive of two major groups of dilambdodonts is the superfamily Erinaceoidea. The molar cusps are simple tubercles; the upper molars have the paracone and the metacone placed close to the lateral margin and, in living members, are squared up through the development of a hypocone. There may be some enlargement of incisor teeth, but the zygomatic arch, although slender, is always retained.

Living members are confined to the Old World. *Erinaceus*, the hedgehog, is the best known; but more generalized ratlike types, such as *Gymnura*, are found in the Malay region. Members of the hedgehog family are found as far back as the Eocene in both Europe and North America. More primitive fossil types are included in the family Leptictidae. Most of the included genera had essentially triangular upper molars; but in all true leptictids, such as *Diacodon* (Figs. 259, *D;* 260, *B*), there is a weak beginning of a hypocone. The leptictids are characteristic of the Eocene and the Oligocene, but an obscure type from the Upper Cretaceous of North America may belong here. That the erinaceoids are an exceedingly ancient group is proved by the presence in the Cretaceous of Mongolia, together with the insectivores already mentioned, of *Zalambdalestes* (Figs. 258, *B;* 259, *B*), a small and very primitive form with tritubercular molars of the orthodox placental type and features which suggest that it is ancestral to the hedgehog group, if not also to other insectivores.

Soricoids.—The living shrews and moles, the superfamily Soricoidea, are characterized by the paracones and metacones forming a W-shaped outer wall on the quadrate upper molars. This feature serves to distinguish them from other insectivores; but otherwise they are structurally not far from the hedgehogs and their fossil allies and presumably have been derived from primitive erinaceoids. The shrews (*Sorex,* etc.) are small, mouselike forms which in their habits and general appearance probably closely simulate the ancestral insectivores. They are, however, considerably specialized in internal structure; for example, the zygomatic arch is incomplete, the middle incisors are elongated, and the lower canine and most of the premolars have disappeared. The moles in a broad sense include not only the true moles (such as *Talpa*) with powerful, highly specialized limbs for digging but also some more primitive forms with a more shrewlike appearance. The moles are in some respects more primitive than the shrews, for there are no enlarged incisors and the zygomatic arch is preserved. Members of both the shrew and the mole families are known as far back as the Eocene; *Proscalops* (Figs. 258, *C;* 259, *E*) is a well-known American Miocene member of the latter group. In the Eocene and Paleocene there were several poorly known little insectivores, such as *Nyctitherium,* which belonged to the soricoid group and which may tend to link it to the still older erinaceoid stock.

Other dilambdodonts.—Certain other forms which are fairly comparable to erinaceoids and soricoids but do not appear to fit readily into either superfamily may be mentioned here. The elephant shrews (*Macroscelides,* etc.) of Africa, small, hopping types with an elongate proboscis, are almost unknown as fossils but are of considerable evolutionary interest. They have many typical insectivore characters but show many similarities to the tree shrews. These latter forms are classed in the present work with the primates, to which their fossil relatives show close resemblances. In the lack of fossil evidence the position of the elephant shrews is questionable.

Pantolestes is a Middle Eocene, North American animal about the size of an otter, apparently predaceous in habits and started on the road toward a water-living type of existence. The braincase was elongate; the face was short and the jaw heavy, the dentition rather carnivorous in character. But the form does not fit into any group of the order Carnivora; the teeth suggest a derivation from primitive erinaceoids. Smaller and more primitive relatives from the Paleocene (*Bessoecetor* [Figs. 259, *G;* 260, *D*]) are in agreement with this suggested derivation, and hence the pantolestoids may be considered as constituting a superfamily of the dilambdodonts.

Mixodectids.—Other groups to be mentioned are more remote from either primitive or typical insectivore assemblages but may be included in the order as representatives of widely divergent lines which, however, hardly merit separate ordinal classification. In this category we may mention *Mixodectes* and its relatives of the Paleocene and Eocene of North America. These imperfectly known forms have been variously assigned to the rodents and to the primates. They have enlarged anterior teeth, analogous to those of rodents; but there are no other rodent features, and chisel-like incisors have, as we shall see, evolved independently a number of times among the placentals. The cheek teeth (Figs. 259, *F;* 260, *C*) are sharp cusped, whereas those of primates tend to a more bunodont nature. Probably the mixodectids represent a short but sterile side branch of the early placental stock and, as such, are best considered as aberrant insectivores.

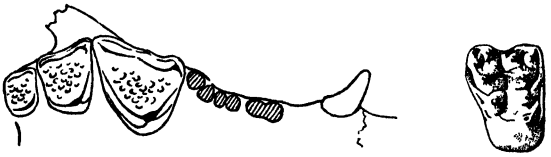


FIG. 261.—*Left*, right upper cheek teeth of *Zanycteris*, a Paleocene insectivore with teeth resembling those of a specialized modern bat group. (×2½). *Right*, an upper molar of *Plagiomene*, a Lower Eocene relative of the "flying lemur" (×3 approx.). (After Matthew.)

A number of other genera, or groups of genera, of placental mammals, mainly from the Paleocene or Eocene, are similarly difficult to place—they do not fit well into the evolutionary scheme of other groups and hence may be left in the insectivores for want of any other place to put them. As an example, we may cite *Zanycteris* (Fig. 261) of the North American Paleocene, with small premolars but with greatly expanded molars covered with numerous small, indistinct cusps. These teeth are very similar to those of Recent leaf-eating bats of South America. But it is highly improbable that this particular bat type was in existence at such an early date; *Zanycteris* is probably merely analogous in dental structure and can best be disposed of by using the order Insectivora as a dumping ground for it and for other anomalous genera.

The "flying lemur."—Living today in the East Indian islands is *Galeopithecus*, the "flying lemur," a herbivorous, tree-living form about the size of a large squirrel. The popular name cannot be called appropriate, for the animal is not a lemur nor does it fly. It is, however, the most highly developed of any of the mammalian gliding forms. A very large membrane stretches from the neck to the hand and foot and onto the tail, enabling the animal to "plane" for a considerable distance. The upper molars are triangular in shape but peculiarly constructed, with three outer and two inner cusps, this arrangement reversed below, and a general tendency for multiplication of small cusps. *Galeopithecus* is not an ancestor of the bats but may represent morphologically a stage in the development of the bat type of flying apparatus. The fingers are not greatly elongated (although webbed) and retain claws, but the hands are rather large as compared with the animal's bulk.

Through most of the Tertiary there is no record of this interesting type. But in the late Paleocene and the Lower Eocene of North America have been found several inadequately known forms, such as *Plagiomene* (Fig. 261), with molars of similar structure. The "flying lemur" and its fossil relatives form the Dermoptera, often considered a separate order but here included in the Insectivora, since, except for the development of a flying membrane, the structural features are not incompatible with those of the present group.

Bats.—Only in the bats—the order Chiroptera—has true flight been developed by mammals. As in the pterosaurs (and in contrast with birds), the wings are formed by webs of skin; but, instead of their being supported by a single elongate finger, nearly the whole hand is involved. The thumb, a clutching organ, is free and clawed; the other four fingers are all utilized in support of the wing membrane; claws are lost on these fingers (except the second in fruit bats); and, as would be expected, the end-phalanges are reduced and may be absent. In having the wing expanse broken by the long digits, the bat has evolved a more flexible and less easily damaged wing than that of the pterosaur. In connection with the bat's habit of hanging by the hind legs, those structures, as well as the pelvis, are peculiarly developed but rather weak.

The orbit is but rarely closed behind. All the teeth (Fig. 262, *B*, *C*) may be present except for an upper incisor and the first premolar, but the anterior teeth may be considerably and variously reduced. The greater number of the bats are insectivorous types, the lower molars being tribosphenic, while the upper molars are often of the old triangular shape or a squared type with a W-shaped ectoloph, a large protocone, and a smaller hypocone. But there is considerable variation in molar structure, for the diet in the various forms ranges from insects and fruit to fish and blood.

The sense of hearing is always highly developed (the auditory region of the skull is greatly swollen), and in many cases grotesque fleshy outgrowths occur about the ears and nose, housing delicate tactile sense organs—adaptations obviously connected with the usually nocturnal flying habits of the group.

The bats are divided into two suborders. The Megachiroptera, the fruit-eating bats or "flying foxes," are large Old World tropical forms. They are little specialized in most respects, never having the peculiar ear and nose ornaments already mentioned, and with a long, foxlike face. In connection with the fruit-eating habits, the teeth, especially the molars, are often specialized. Except for a form from the Oligocene of Italy, we have no record of their history.

Vastly larger in the number of contained types is the suborder Microchiroptera, comprising all other bats. Typically small insect-eaters, as were presumably the ancestral chiropterans, there is a considerable range of diet in the various families. The incisors tend to be specialized and reduced; in connection with this and with the frequent development of nasal excrescences, the premaxilla is usually small or vestigial, the face is short, and there is a large nasal opening (Fig. 262, *A*).

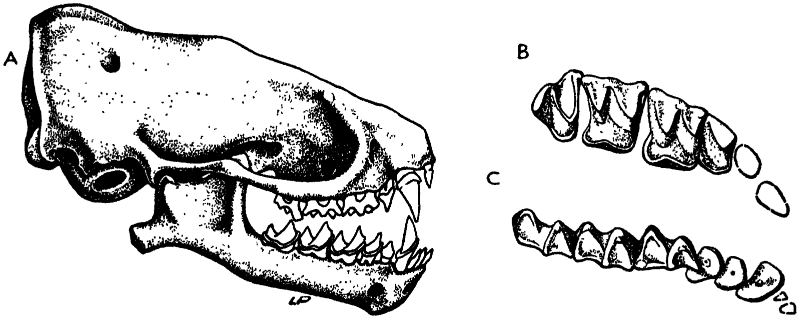


Fig. 262.—Bats. *A*, Skull of member of the existing genus *Nyctinomus* from the Miocene of Europe, skull length about ⅝ inches; *B*, *C*, upper and lower teeth of the same, about 6 times natural size. (After Revilliod.)

It is possible that some of the known insectivorous genera of the Paleocene were bats or at least types ancestral to them. But so close are some of the bats to the insectivores in dental characters that we cannot confirm or reject such suggestions in the absence of knowledge of limb and body structure. Flying adaptations must certainly have developed in the Paleocene, for Middle Eocene deposits in both Europe (Fig. 263) and North America have yielded skeletons of microchiropterans with well-developed wings. The American form is more primitive than typical members of the suborder, for the claw on the second finger was still present. By the end of the Eocene and the beginning of the Oligocene the evolution of the varied modern families of bats was far advanced, for representatives of a number of modern groups were present in Europe. Fossil chiropterans are found here and there throughout the Tertiary and in the Pleistocene, but it is only rarely that much except teeth and jaws is found of these small and delicate forms.

It seems obvious that the bats, essentially insectivorous in their beginnings, have been derived from an arboreal insectivorous group, for in such features as are not connected with flight the bats might well be included in the order Insectivora, and certain anatomical considerations suggest relationships with the primates, likewise to be considered as intimately related to the insectivores.

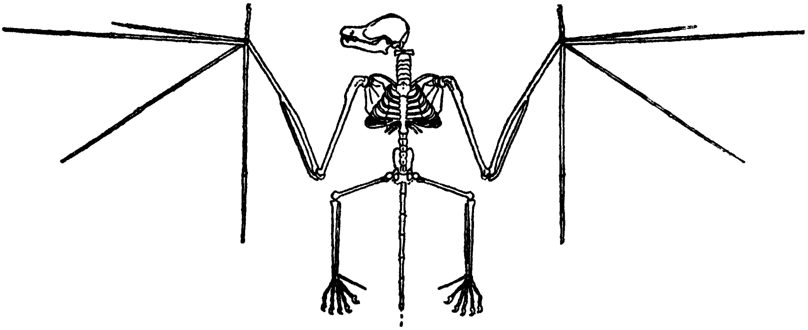


FIG. 263.—Skeleton of a fossil Eocene bat, *Palaeochiropteryx*. (From Revilliod.)

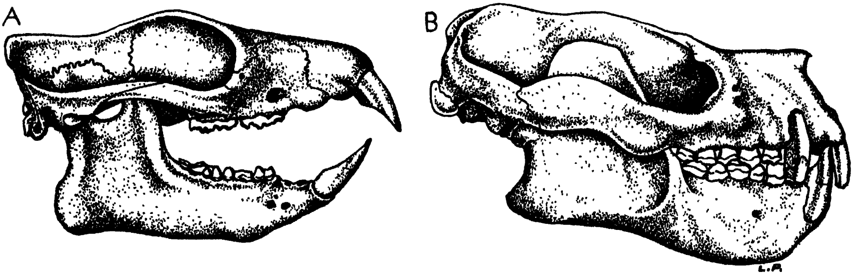


FIG. 264.—Aberrant Eocene placentals. *A*, *Tillotherium*, a Middle Eocene tillodont, skull about 13 inches long; *B*, *Psittacotherium*, a Lower Paleocene taeniodont, skull about 9½ inches in length. (*A* after Marsh; *B* after Wortman.)

Taeniodonts.—An obscure Tertiary group constituting the order Taeniodontia may be considered here for want of a better connection. The order includes but a few forms from the Paleocene and Eocene of North America; they comprise a short-lived archaic outgrowth of the primitive insectivore stock. Such an end-type as *Stylinodon* from the Middle Eocene was comparatively large for its day, the skull reaching a foot or so in length. All the teeth had become high-crowned, rootless, simple pegs growing from a persistent pulp, and the enamel covering was limited to bands along the sides of the teeth. Only a single pair of rodent-like incisors (the lateral) was retained, but the canines were well developed. The skull was short, the jaws deep and powerful; a leaf-eating mode of life has been suggested for these forms. The limbs in later taeniodonts were short and stout, the toes reduced, and powerful claws developed. Somewhat earlier forms, such as *Psittacotherium* (Fig. 264) of the Torrejon and *Calamodon* of the Wasatch, were more primitive in that the teeth (except perhaps the canine) were still rooted and the molars enamel covered, while the Paleocene *Conoryctes* and *Onychodectes* (Fig. 265, *B*) were so close to the insectivore ancestors that it is difficult to decide in which group to place them. In the early taeniodonts the skull was still of primitive shape, long, and low with long and not particularly deep jaws; the teeth were not merely rooted and enamel covered but still retained much of the tribosphenic molar pattern of the early insectivores; and the limbs were slender and primitive in nature. Except for the loss of the central incisors, there was little in these forms to show that they were incipient taeniodonts.

Obviously, the group constitutes an early "experiment" on the part of the insectivore stock in the creation of a herbivorous form with grinding teeth. Taeniodonts, however, were seemingly never common and soon disappeared when placed in competition with the herbivorous ungulates. They have sometimes been confused with the tillodonts, next to be considered. Some writers have suggested that they are related to the edentates, the so-called "toothless" mammals; they have some resemblances to the ground sloths, but, except for a partial loss of enamel from the teeth, these resemblances are of a superficial nature.

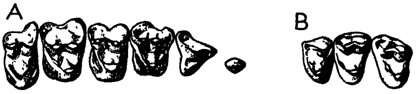


FIG. 265.—*A*, Upper cheek teeth of *Esthonyx*, a primitive tillodont ($\times \frac{2}{3}$ approx.); *B*, upper molars of *Onychodectes* ($\times \frac{3}{4}$) to show the tritubercular origin of the teeth of taeniodonts. (*A* after Cope; *B* after Wortman.)

Tillodonts.—Here, too, may be mentioned the order Tillodontia, another short-lived archaic offshoot from the base of the placental stem. An end-form, *Tillotherium* (Fig. 264), of the Middle Eocene of North America, was the size of a brown bear. The skull, carnivore-like in general proportions, was long and low, the snout slim, the braincase small. The second pair of incisors in both jaws was enlarged and rootless, much as in rodents; the canines were tiny; and the low crowned molars suggest a herbivorous or omnivorous diet. The beast had plantigrade-clawed, five-toed feet and presumably a rather bearlike gait. Lower Eocene forms were much more primitive; *Esthonyx* (Fig. 265, *A*) was less than half as big as the Middle Eocene type, the incisors not so disproportionately large and still rooted. The tillodonts have sometimes been grouped with the rodents, but there is no reason for considering them related except for the large gnawing incisors, a feature which developed in many groups of mammals.

CHAPTER 18

PRIMATES

THE order Primates is of especial interest, since its members include not only lemurs, monkeys, and apes but man himself. Unfortunately, however, fossil remains of this group are more rare than is the case in any other large group of mammals. The reasons for this paucity of material are fairly obvious. Primates are, for the most part, tree dwellers; deposits in which fossil vertebrates are to be found are not normally formed in forested regions. Again, primates are mostly dwellers in the tropics, whereas most of the known Tertiary fossil beds are in what are today zones of temperate climate. It is only in Eocene times, when these regions (as shown by the vegetation) knew tropical conditions, that primates are found to any extent in the fossiliferous deposits of Europe and North America.

The primates are commonly divided into three major groups: (1) the suborder Lemuroidea, including the tree shrews and lemurs, typically small, four-footed forms of rather squirrel-like appearance, found today in the Old World tropics but present in the Eocene in Eurasia and North America; (2) the suborder Tarsioidea, which includes *Tarsius*, a curious, small, hopping, ratlike creature from the East Indies, and its fossil Paleocene and Eocene relatives, occupying a position structurally intermediate between lemurs and higher primates; (3) the suborder Anthropoidea, comprising the South American monkeys, the more advanced monkeys of the Old World, the great manlike apes, and man.

Primates are essentially arboreal, only a few forms (such as the baboons and man) having returned to a life on the ground. There is considerable evidence suggesting that the primitive placentals were tree dwellers to begin with and that the primates have merely continued on in this ancestral track. Arboreal life is apparently responsible for much of the progressive development of primate characteristics; and, although man is not a tree dweller, this life of his ancestors has left its mark deeply upon him and is perhaps in great measure responsible for his attainment of his present estate.

Arboreal adaptations: limbs.—Locomotion in the trees has left the postcranial skeleton of the primates in a condition much closer to that of the primitive placentals than is the case in most groups. Flexibility is necessary for climbing trees, and there is none of the restriction of limb movement to one plane found in ungulate groups and in many carnivores and rodents. Very rarely is there any reduction or fusion of bones in the lower segment of the limbs. The clavicle is retained, in contrast with running forms, its connection of shoulder with trunk relieving the strain on the muscles when the animal is suspended from a limb.

In contrast with such arboreal types as the squirrels, in which climbing is accomplished by digging the claws into the bark, the primate hold is generally accomplished by grasping boughs or twigs. The claws characteristic of primitive mammals have been in most cases transformed into flat nails serving as a protection to the finger tips; claws, however, still persist in various instances in lemuroids and even marmosets.

In primitive placentals the pollex and hallux were presumably somewhat divergent. This grasping characteristic has usually been retained and emphasized in primates (Fig. 248). In most cases it is the hallux which is the most highly developed and divergent and hence more opposable to the other digits. In contrast, the thumb is sometimes reduced, or even absent, in forms which habitually progress by swinging from branch to branch, the other four fingers here hooking over the bough and the thumb not only being useless but actually in the way. Otherwise, there has been but little reduction of digits; the primates are in this respect more conservative than most mammalian groups.

Quadrupedal locomotion is the rule among primates, bipedal tendencies becoming apparent for the most part only among the higher members of the order. The hands, however, while primarily possessing their grasping adaptation in relation to locomotion, are well adapted (almost alone among mammals) for grasping food and other objects; and even among the lemurs there is a tendency toward a sitting posture and the release of the front feet from supporting the body.

The primitively long tail is retained in almost all the lower primates and is apparently of considerable use in balancing. In many South American monkeys it has developed into a prehensile "fifth hand." In a number of cases, however, the tail is reduced or absent, and there is no external tail in the manlike apes and in man.

Teeth.—An omnivorous diet appears to have been general in early primates, and similar food habits characterize many living types (although there has been a strong herbivorous trend). The dentition (Figs. 266, 267), hence, is usually less specialized than in most mammalian groups. Tree shrews may retain all three of the incisors present in primitive mammals; no more than two are present in other primates, and these may be variously modified and reduced in lemurs. The canines are usually unreduced, projecting moderately above the other teeth, and are often larger in the males.

While four premolars are present in a few primitive fossil forms, no living primate possesses more than three; and the higher members of the order have but two. Related to this is a shortening of the tooth row evident in the group as a whole, although (as in the baboons) there may be a secondary lengthening brought about by elongation of the molars. The premolars are never molarized and are typically bicuspid.

The molars of the most primitive forms (Fig. 241, *A*) are often very similar to those of the early placentals, showing clear traces of the primitive triangular pattern; but the originally sharp cusps have tended to soften down to a bunodont condition. A hypocone is usually added above. Below, as in many other groups, the paraconid disappears to give an essentially four-cusped tooth; but a hypoconulid on the back margin is persistent in many cases, and even in man this fifth cusp is often present. There is little tendency toward a hypsodont condition, since the food is mainly of the softer kinds, such as fruit and buds.

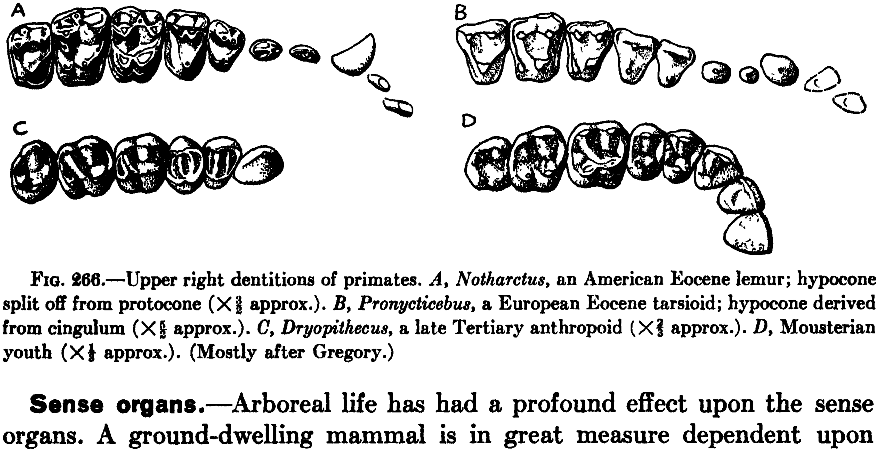


FIG. 266.—Upper right dentitions of primates. *A*, *Notharctus*, an American Eocene lemur; hypocone split off from protocone ($\times\frac{3}{2}$ approx.). *B*, *Pronycticebus*, a European Eocene tarsioid; hypocone derived from cingulum ($\times\frac{5}{8}$ approx.). *C*, *Dryopithecus*, a late Tertiary anthropoid ($\times\frac{2}{3}$ approx.). *D*, Mousterian youth ($\times\frac{1}{2}$ approx.). (Mostly after Gregory.)

Sense organs.—Arboreal life has had a profound effect upon the sense organs. A ground-dwelling mammal is in great measure dependent upon smell for his knowledge of things about him, and his olfactory organs are highly developed while sight is usually comparatively poor. The reverse is true in these arboreal types. For locomotion in the trees good eyesight is essential; and throughout the primate group there has been a progressive series of advances in the visual apparatus. Even in the lemurs the eyes are large, and there is a tendency to rotate them forward from their primitive lateral position. This results, in such forms as *Tarsius*, in a condition in which the two fields of vision are identical. With the overlapping of visual fields, there results in primates, as in other groups of mammals, a sorting-out of nerve fibers so that, instead of two mental pictures, one for each eye, there is a doubling-up of the impressions from the common field of sight, giving stereoscopic vision with its effect of depth. In no other group of mammals is the overlap of fields so great; in all higher primates (as in ourselves) the stereoscopic effect is complete. In addition to this improvement, already initiated in *Tarsius*, the Anthropoidea have created in each eye a special central area in which detail is much more clearly seen.

With this increase in vision goes a corresponding decrease in the sense of smell. Even in the lemurs the olfactory sense is reduced, and in the manlike apes and man it is probably in the most rudimentary state to be found in any land-dwelling placental.

Brain.—The brain, as well, has been profoundly influenced by arboreal life. Locomotion in the trees requires great agility and muscular co-ordination, which in itself demands development of the brain centers; and it is of interest that much of the higher mental faculties is apparently developed in an area alongside the motor centers of the brain. Again, the development of good eyesight rendered possible for primates a far wider acquisition of knowledge of their environment than is possible for forms which depend upon smell. Perhaps still more important in the development of primate mentality has been the development of a grasping hand. This is not only an advantage in feeding but undoubtedly has contributed materially to primate mental development through the knowledge gained by the examination of objects.

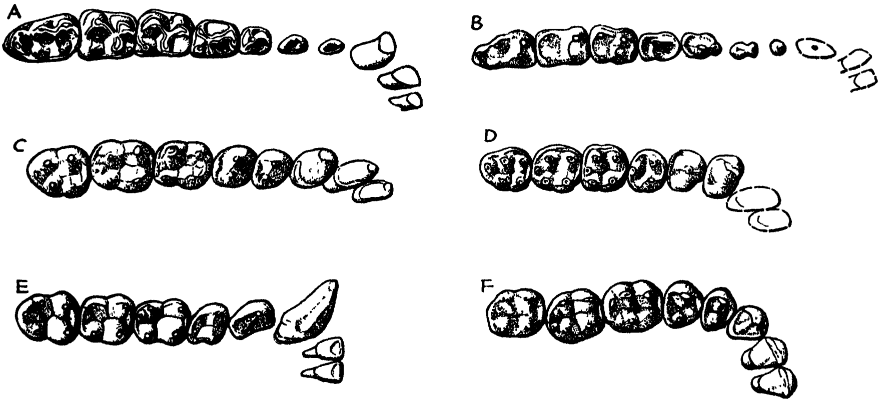


FIG. 267.—Lower left dentitions of primates. *A*, *Notharctus*, an Eocene lemur ($\times\frac{3}{2}$ approx.); *B*, *Pronycticebus* ($\times\frac{5}{2}$ approx.); *C*, *Parapithecus*, an Oligocene Old World monkey ($\times\frac{5}{2}$ approx.); *D*, *Propliopithecus*, an ancestral Oligocene anthropoid ($\times\frac{3}{2}$ approx.); *E*, *Dryopithecus*, a late Tertiary anthropoid ($\times\frac{2}{3}$ approx.); *F*, Mousterian youth ($\times\frac{1}{3}$ approx.). (Mainly after Gregory; *C*, *D* after Schlosser.)

A constantly increasing brain size has been a characteristic feature of primate development. The cerebral hemispheres have grown in size and in all the higher Anthropoidea completely cover the cerebellum. Among the smaller monkeys are to be found the highest relative weights of brain to body in mammals.

Skull.—These changes in dentition, sense organs, and brain have been associated with great changes in the primate skull. Tree shrews and many lemurs have an elongate skull of primitive appearance, with a long facial region and a long, low braincase. But with the reduction of the sense of smell and the concurrent abbreviation of the tooth row, the muzzle in most primates has shortened considerably, the face sloping downward toward the mouth at a considerable angle. The orbits were rather large in even the most primitive of the lemurs, and even in the Eocene were almost invariably bounded posteriorly by a postorbital bar—a feature in which they were in advance of almost all known forms of that period. In the higher lemurs the orbits tend to turn forward, their median boundaries crowding close together above the nostrils—a position in which they are found in all higher primates. The originally superficial bar separating orbit and temporal opening becomes in the higher forms a solid partition. In many forms the upper margin of the orbits is above the level of the braincase, projecting as a supraorbital ridge.

The expanding brain naturally requires an enlarged braincase; and, except for some primitive types, the primate braincase tends to be high vaulted and rounded. Sagittal and occipital crests, present in the early lemurs, are rare in later and higher types, for with expansion of the braincase the temporal muscles, between which the crests form, fail to meet. These crests are to be found only in the larger forms and in the heavily muscled, herbivorous types. The occipital condyles are usually shifted in a varying degree from the back to the under side of the skull. In the trend toward erect posture in higher primates the skull tends to assume a roughly globular shape and to be balanced on the upper end of the vertebral column. The two halves of the lower jaw, primitively loosely connected, become fused in higher types.

Tree shrews.—It is generally agreed that the living tree shrews of the Orient are forms transitional between the primitive insectivore ancestors and more typical primates. They may be reasonably placed in either order, but we here follow current tendencies in ranging them as basal members of the primate stock. They are small, arboreal animals with a squirrel-like appearance; anatomically they show a mixture of primitive features with others suggestive of relationship to primates and, particularly, the lemurs. Claws, rather than nails, tip the toes; three incisors are present in the lower jaw of living tree shrews; the cheek teeth are quite primitive in character. On the other hand, the presence of a relatively large brain in which the olfactory region is small, a postorbital bar, a middle-ear region built like that of lemurs, and considerable opposability of pollex and hallux all indicate that the tree shrews are allied to the ancestry of the more typical primates. Unfortunately, there are few early fossils that can be assigned with confidence to the tree-shrew group. The only adequately known form which appears to be closely related is *Anagale* (Fig. 268, *D*) of the Oligocene of Asia. This genus shows a minor but interesting advance in that nails had developed in the hind foot, at least; on the other hand, *Anagale* is a step below the living tree shrews in that the postorbital bar is incomplete and there is a full complement of incisors.

Eocene lemurs.—Apart from the transitional tree shrews, the living primates below the monkey level comprise a varied series of lemurs (mainly from Madagascar) and *Tarsius* of the East Indies. The lemurs are seemingly primitive forms; *Tarsius,* although specialized, is believed to represent a more progressive stage in primate evolution, transitional to the Anthropoidea.

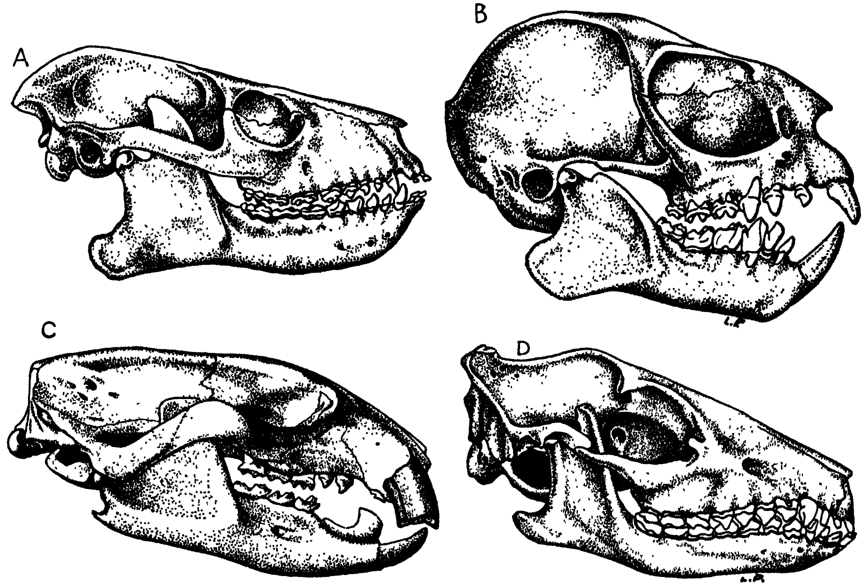


FIG. 268.—Skulls of early primates. *A*, *Notharctus*, an Eocene lemur, length of skull about 3 inches; *B*, *Tetonius*, an Eocene tarsioid, length of skull about 1⅛ inches; *C*, *Sinclairella*, an early Oligocene primate with enlarged incisors, length about 2¼ inches; *D*, *Anagale*, an Oligocene relative of the tree shrews, length about 2½ inches. (*A*, *B* after Gregory; *C* after Scott and Jepsen; *D* after Simpson.)

Almost nothing is known of the antecedents of these living groups in the later Tertiary. In the Paleocene and the Eocene, however, there are, in both North America and Europe, numerous genera of small mammals which are obviously primitive primates ancestral to both modern stocks. The taxonomic assignment of many of these forms has, however, been a difficult one. Most of the remains are very fragmentary and consist of teeth and partial jaws. Primate teeth are rather primitive in nature, and dental differences between lemurs and tarsioids are not marked; it is, therefore, not surprising that many of these genera have been variously and variably assigned to the insectivores, lemurs, and tarsioids.

There was, apparently, a strong tendency among early primates for the development of long, chisel-like incisors analogous to those of rodents or of the multituberculates and diprotodont marsupials already discussed. As will be seen, such teeth occur in one of the living Madagascar lemurs, and some tendency of this sort was present in early types which are rather confidently believed to be true tarsioids. In the Paleocene and Eocene, such developments were very common. *Carpolestes*, *Apatemys*, and *Plesiadapis* (Fig. 269) are forms which have very highly developed incisors but differ so among themselves that each is regarded as representative of a separate family of aberrant early primates. The *Carpolestes* type, confined to the Paleocene of North America, has, in addition, developed large, shearing lower premolars, which strengthen the analogy with certain multituberculates and diprotodonts. The other two groups are present in Europe as well as in North America, and one apatemyid survived into the American Oligocene (*Sinclairella* [Fig. 268]). As our remarks on dental similarities would suggest, the exact relationships of these families are obscure. *Carpolestes* and *Apatemys* are perhaps more closely related to the tarsioids; the plesiadapids have been thought to be aberrant lemurs or tree shrews.

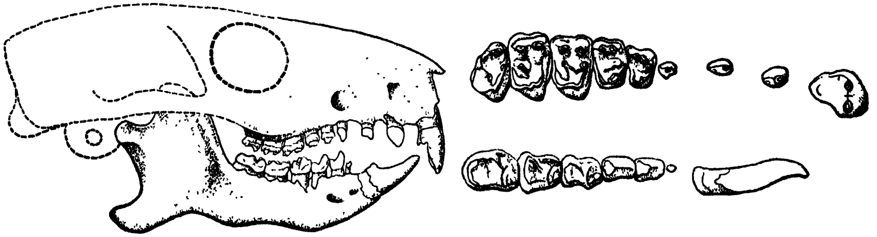


FIG. 269.—*Plesiadapis*, a late Paleocene primate with enlarged incisors. The skull is imperfectly known. Skull about natural size, teeth ×2 approx. (After Matthew and Simpson.)

Despite doubts as to the position of many genera, there are a number of Eocene forms which are generally accepted as definitely lemuroid and ancestral to the typical living lemurs. These constitute the family Adapidae, of which *Notharctus* of North America and *Adapis* and *Pronycticebus* of Europe are among the better-known types (Figs. 248; 266, *A*, *B*; 267, *A*, *B*; 268, *A*). *Notharctus* was a small mammal with a skull about 2 inches long which probably resembled the ordinary lemurs of today in general appearance. It was already quite lemur-like in its proportions and many structural features. The dentition, however, was more primitive in a number of respects. Although some members of the family had but three premolars, *Notharctus* still retained the full complement of four. Further, the upper incisors were comparatively normal; the canines were of primitive type; and the lower incisors little, if at all, procumbent. In *Notharctus* a hypocone had already developed in the upper molars, but some Eocene relatives had only slight traces of this structure. In the European forms a hypocone was developed as well; but a curious feature is that, while the two forms were closely related and had both acquired this same new cusp, *Adapis* and *Pronycticebus* had obtained it by an upgrowth of the cingulum, *Notharctus* by a budding-off from the protocone.

Madagascar lemurs.—By the close of the Eocene the lemurs had disappeared from the fossil record in the North Temperate Zone, and we know nothing of their further history until Pleistocene and Recent times. Here we find them present in Old World tropical regions, where conditions today are probably not dissimilar from those prevailing farther north in the Eocene. The main center of the group is the island of Madagascar. This region presumably was cut off from the mainland during most of the Tertiary; and there are but few carnivores—a fact which may have been responsible for the survival of these primitive primates (as well as of many insectivores).

The Madagascar lemurs may all be included in the family Lemuridae, using this term in a broad sense. They are of interest in giving us as near an approach as we can obtain today to the general appearance, habits, and structures of our Eocene primate ancestors. A typical Madagascar lemur of today is a fairly small arboreal animal, nocturnal in habits, with a bushy hairy covering which contrasts with the rather sparse coat of most higher primates. The limbs are moderately long, the ears pointed, and the eyes are directed more laterally than forward. The lemur tail, usually long, is never a grasping organ. Pollex and hallux are always widely separable from the other fingers; the big toe is especially well developed and has a flat nail in all forms, whereas the other digits are variable in their covering. Typical lemurs have a clawlike nail on the second toe but normal nails on the other digits.

In living lemurs the upper incisors are often small or absent, while the lower ones, together with an incisor-like canine, slant forward as a fur-combing organ. The upper molars vary from the triangular to the quadrangular pattern.

The lemur face may undergo some shortening, but it is in most cases a comparatively long and foxlike muzzle. The braincase is long and low in the more primitive living types but somewhat expanded in the more advanced lemurs.

There are numerous divergences from this general type among the living Madagascar lemurs. There is, for example, a small, hopping form; and *Indris* and a few other lemurs are rather large and somewhat monkey-like in superficial features. Still other variants have been discovered in Pleistocene bog deposits on the island. *Megaladapis* was the largest-known lemur, attaining the size of a pig, with a skull a foot long, peculiarly long and decurved nasal bones, and small eyes; it seems to have resembled the Eocene lemurs closely in many features. A second extinct group was represented by *Archaeolemur*, also large for a lemur (a 5-inch skull) but with large eyes turned remarkably far forward and a large brain, there being no sagittal crest. The face was considerably shortened. This extinct form paralleled in a number of respects the higher primates and is one of several abortive "efforts" of the lemur group to reach a monkey status.

A final member of the Madagascar primate fauna is the aye-aye, *Chiromys*. It is a nocturnal form about the size of a small cat, with a short, high skull of the shape found in the higher lemurs and monkeys. All the digits except the big toe have clawlike structures rather than nails; the middle finger is very long and slim and is said to be used to extract grubs from their holes in the wood. The single remaining pair of incisors is enlarged in rodent fashion and is used in gnawing through bark in search of insect food. The aye-aye has been thought to have descended from the plesiadapids but more probably has resulted from a parallel evolution among the Madagascar lemur group.

Higher lemurs.—All the living non-Madagascar lemurs are included in a higher group, the family Lorisidae. The lorises of the Indian region are typical; in Africa the group is represented by the "bush baby," *Galago*, and the potto. The muzzle is rather short, the braincase high, the eyes turned somewhat forward, and the premolars reduced to two; the lower front teeth, however, have the typical arrangement of the Madagascar lemurs. The index finger is reduced, giving a better grasp between the thumb and the remaining fingers. The advanced skull structures of these lemurs are of the sort required to turn a lemur-like primitive primate into a more advanced type; but it is generally held that this is a development parallel to, and not on, the main evolutionary line. It is sometimes thought that the lorises, because of technical differences in construction of the ear bulla, are only remotely related to the more typical lemurs; but this belief lacks paleontological support and neglects embryological considerations.

Tarsius.—A small but very interesting primate group is that which includes a single living animal, *Tarsius*, in addition to numerous Paleocene and Eocene fossil genera. These forms have often been classed as lemurs but are quite advanced in structure and may be appropriately placed in a separate suborder, the Tarsioidea, intermediate between the true lemurs and the Anthropoidea.

Tarsius is a small, nocturnal, tree-living form from the East Indies. The tail is very long, and the hind legs are adapted for a hopping gait. The braincase is large and rounded, and the foramen magnum is pushed somewhat forward onto the under side of the skull in contrast to the usual lemur condition. The visual apparatus is much more advanced than that of the lemurs. The eyes are exceptionally large and are turned completely forward from the primitive lateral position, with the orbits very close together above the nose.

In ordinary lemurs there is only a superficial bar separating orbit and temporal fossa; but in *Tarsius* the alisphenoid extends outward below the frontal and jugal and closes off the greater part of the opening between the two regions, much as in the Anthropoidea.

While vision has thus advanced, the sense of smell has been proportionately reduced. The foxlike snout of the typical lemur has disappeared, and the nose is reduced to a small nubbin tucked in beneath and between the eyes. There is little projection of the muzzle (the tooth row is rather short); and we have here the beginning of the type of face found in monkeys, apes, and man. There are some specializations of the front teeth, but the cheek teeth are of primitive pattern with fairly typical tribosphenic molars.

Specializations have developed in connection with the hopping gait. Alone among primates we find in *Tarsius* a partial fusion of tibia and fibula. A third segment is introduced into the limb by means of an elongation not of the metatarsals but of the calcaneum and navicular (a similar development has occurred in a Madagascar lemur and in *Galago*). This seemingly odd fashion of developing a third joint is readily understandable when we consider the situation. The ordinary animal which introduces an extra segment for hopping or, indeed, fast locomotion of any sort (as the kangaroo, jumping mice, or any typical ungulate) has no grasping ability and is usually a ground-living type. The primate, however, is in great measure dependent for security in the trees on the powers of opposability of the great toe. If the metatarsals were to elongate, his grasp would be lost; elongation must take place proximal to the origin of the big toe, and the proximal tarsal bones give the only possibility for this development.

Apart from this peculiar limb specialization, *Tarsius* is close to the higher primates in most features. An additional suggestion that this form is a relic of a primitive group transitional to the Anthropoidea lies in the structure of the placenta. In the lemurs this structure was of a type probably present in primitive placentals. But in *Tarsius* the placental connections between mother and young are concentrated into a pancake-shaped structure which is shed at birth as in the higher primates.

Eocene tarsioids.—Prior to Recent times there is a gap in the history of the group extending to the early Tertiary. But in Paleocene and Eocene deposits we find in Europe and North America numerous remains of small forms unquestionably related to *Tarsius*, as well as others of rather more doubtful position. Many of them are known merely by the dentition. This was often, as in *Tarsius*, close to the primitive placental type in molar construction, the hypocone appearing only rarely. In some genera the first lower premolar was still present as a small tooth; but normally there were, as in *Tarsius*, but three premolars, and in one case there were but two. The anterior teeth, however, were quite variable in structure. In such forms as the best-known genera, *Tetonius* (Fig. 268, *B*) of the American Lower Eocene and *Necrolemur* of the Upper Eocene of Europe, the incisors show some of the enlargement noted in various other lines of early primates.

In *Tetonius* the general structure of the skull is quite similar to that of the living *Tarsius*, with a very short face and huge, forwardly turned orbits with a developing partition behind them. Some of the others, like *Necrolemur*, appear to have been rather more lemur-like, with a somewhat less reduced snout.

These early tarsioids are customarily included in the family Anaptomorphidae, within which, however, there certainly existed a diversity of types, and some of the earliest Paleocene genera may have been close to the ancestry of the lemurs as well as tarsioids. Eocene tarsioids had specialized in a number of directions. In one or two forms skeletal material shows that the peculiar modifications of the hind legs found in the living *Tarsius* were already present. Still others may be ancestral to the higher anthropoid primates which had developed by the beginning of the Oligocene.

Anthropoids.—All the remaining primates—monkeys, apes, and man—may be placed in the suborder Anthropoidea, the manlike primates. In all of them we have a very distinct advance upon the types already discussed. The eyes are large and face forward, as in *Tarsius*, and the orbits are completely separated from the temporal fossa. The sense of smell is unimportant, and the snout is greatly reduced.

The monkey normally is a four-footed walker, but there is a great tendency for an upright sitting posture and the freeing of the hands for the manipulation of food and other objects. The tail is variable; in some South American types it is prehensile, but in the higher forms it is frequently reduced.

There are never more than three bicuspid premolar teeth, and the higher Old World forms have but two. The last molar tends toward reduction and is actually lost in one monkey family. The upper molars are still tritubercular in a few of the more primitive forms, but generally the typical quadrate pattern is developed in both jaws.

The brain is comparatively large in all the members of the group. The braincase is typically much expanded, and crests are only exceptionally developed. The foramen magnum tends to be under, rather than at the back of, the skull, with the face turned forward almost at right angles to the backbone. The two halves of the jaw are fused.

The suborder may be divided into two groups, isolated geographically both at the present day and in the past, as far as our knowledge goes. The more primitive infraorder, the Platyrrhini, are the monkeys of South America; the Catarrhini include the more advanced monkeys, apes, and man, all of which have their home in the Old World.

South American monkeys.—The Platyrrhini comprise two families of monkeys now living and found as fossils only in South and Central America. Superficially, many are quite similar in appearance to Old World monkeys but seem to be more primitive in a number of respects. They are, on the average, much smaller than their Old World relatives. Almost never is there any reduction of the primitively long tail. The thumb is but little opposable to the other fingers. Three premolars are still present in all cases, whereas the oldest fossil representatives of the Old World apes had already lost the second premolar. The group name ("flat nose") refers to the fact that the nostrils are usually far apart and face outward.

Marmosets.—Of the two families, the smallest both in number of forms and in the size of the individuals is that of the marmosets, the Hapalidae. *Hapale*, the common marmoset, is a small creature, squirrel-like in size and general appearance, with thick fur and a bushy tail. Squirrel-like, too, is the fact that the toes (except the hallux) have the nails compressed and clawlike, so that the progression is mainly by digging the claws into the bark; the hallux has lost much of its opposability. A peculiar feature is the fact that the last molar has been lost, the only case of its complete reduction among primates (although man is approaching this condition). The incisors, and the lower canine with them, are rather procumbent and lemur-like. A Miocene marmoset has been recently reported, but otherwise the early history of the family is unknown. Some have believed that these creatures are the most primitive of anthropoids, but such features as the molar loss suggest that they are specialized rather than primitive.

Cebids.—A more important and larger group is that of the Cebidae, the typical South American monkeys. Here the size is somewhat larger, the hairy covering somewhat thinner (a tendency carried much further in Old World types), and the teeth are little specialized and with the full anthropoid complement of three premolars and three molars. In some cebids, alone among primates, a prehensile tail has developed.

Most primitive of living cebids is the group represented by *Aotus* [*Nyctipithecus*], the owl monkey or dourocouli, a small form with a presumably primitive thick woolly covering and a small brain. It is a nocturnal form, while most monkeys are active in the daytime. (Parenthetically, this raises the question as to whether the primitive primates were nocturnal, for this is the case in *Tarsius* and almost all of the lemurs.) The owl monkey is quite similar to the marmosets and may be close to the base of the platyrrhines. This belief is strengthened by the fact that the only cebid of any antiquity, *Homunculus* of the Miocene, belongs to this group.

The owl monkeys and several other fairly primitive forms lack a prehensile tail. This "fifth limb" is developed in the remaining cebids. Of these, the commonest group is that best known through the capuchin monkey, *Cebus*, usually to be found accompanying the organ-grinder. Closely related are the spider monkeys, *Ateles*. Here the limbs are very long and slender, the thumb reduced or absent, the nails rather clawlike. These monkeys are clever acrobats, swinging from the branches by any of their five useful appendages.

A final group is that of the howling monkeys, *Alouatta*. These are the largest of the New World forms, some as large as a good-sized dog, and are leaf-eaters with heavy molar teeth. The larynx is expanded into a huge ossified shell, with a resonating chamber within, by means of which night is made mournful in the South American forests.

Little is known, unfortunately, of the fossil history of the South American monkeys beyond the fact that both families were present in the Miocene. South America, as we have noted, seems to have been an isolated area from early Eocene times. Perhaps the ancestral platyrrhines entered South America at the dawn of the Tertiary; forest-dwelling forms of this sort might well have been present, and even abundant, in the Eocene and Oligocene and yet have failed to be preserved in the plains deposits of Patagonia. On the other hand, it is possible that, like the hystricomorph rodents, they managed to gain access to the continent at a later date. Unless some such late entry were made "overseas" from Africa, the platyrrhines must have evolved independently of catarrhines from a tarsioid stock, for no members of the Anthropoidea developed in North America, the only area with which South America was early connected.

Catarrhines.—The catarrhines of the Old World form a well-defined group, including the living monkeys of Asia and Africa, the anthropoid apes and man, and their fossil representatives. The name indicates one of the many features in which they are more advanced than the South American monkeys; the nostrils are closer together and open forward and downward, with a smaller bony opening. There is a rather general tendency toward an increase in size which culminates in the chimpanzee, man, and the gorilla. Although originally arboreal, some of the higher or more specialized types, such as man and the baboons, tend toward a terrestrial life. The tail is often shortened or absent. Primitively four-footed, some have tended to an arm-swinging type of locomotion in which the body is held erect; man has attained an erect posture. Although progression on the ground is usually on all fours, the long arms bring the back into a slanting position, while sitting is the common catarrhine pose when not in motion. The thumb is usually well developed and opposable, and the big toe universally so except where secondarily reduced in man. The hairy covering is always thin and the face naked.

The brain is large; but since the forms are, on the average, larger, the ratio of brain size to body is reduced, and sagittal and occipital crests are more common than in South American monkeys. The face, primitively short, tends to elongate in many instances in correlation with a tendency toward a vegetable diet and a consequent increase in tooth size. The second premolar is always absent, the tooth formula being invariably $\frac{2 \cdot 1 \cdot 2 \cdot 3}{2 \cdot 1 \cdot 2 \cdot 3}$. The molars are quadrangular and essentially four-cusped.

Old World monkeys.—The most primitive known member of the group was *Parapithecus* (Figs. 267, *C*; 270, *B*), from the Lower Oligocene of Egypt. Although it is known only from one jaw, there is yet enough information to be derived from this to tell us that we are dealing with a small, primitive catarrhine which may have been close to the ancestry of the later Old World monkeys and apes. The canine was small, and the first of the premolars was still simple, in contrast with its usual bicuspid condition in catarrhines. There were four main cusps on the molars, but these were not connected by cross-crests, as in the living monkeys; and a fifth cusp, the hypoconulid, was present on all three molars, whereas it appears only on the last in the existing Old World monkeys. The two halves of the jaw met at a sharp angle, a primi-

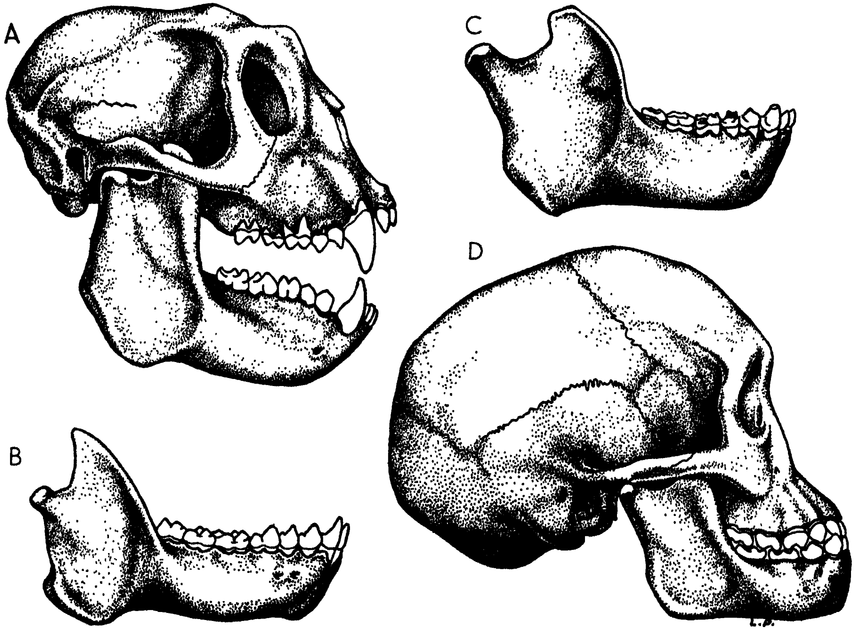


FIG. 270.—*A*, The skull of *Mesopithecus*, a Pliocene Old World langur, length of original about 3 inches; *B*, the jaw of *Parapithecus*, oldest-known Old World monkey from the Lower Oligocene of Egypt, original about 1½ inches long; *C*, the jaw of *Propliopithecus*, oldest anthropoid ape, from the same deposits, original about 2⅝ inches long; *D*, restored skull of *Australopithecus*, a young individual of an extinct anthropoid-ape type from South Africa. (*A* after Gaudry; *B*, *C* after Schlosser; *D* after Dart and Broom.)

tive feature contrasting with the more rounded contour of the "chin" in all living Old World forms. The jaw proportions suggest that the skull, if found, would reveal the presence of large eyes and a large brain. As far as our knowledge goes, this small monkey may well have been the common ancestor of all the later catarrhines. In appearance it might have been similar to the more generalized African monkeys of the present day.

The living members of the Old World monkeys constituting the family Cercopithecidae include a large number of forms with a wide range of structure. They are, in terrestrial locomotion, four-footed forms, walking flat on palm and sole. The more primitive forms are arboreal, but the baboons and their relatives show a progressive tendency toward a ground-dwelling life. Toughened skin areas—the ischial callosities—are present on the buttocks. As noted above, the molars are four-cusped, the hypoconulid being present only on the last lower molar; and, characteristically, two cross-crests are developed.

Two great groups may be distinguished, the larger being that of the subfamily Cercopithecinae. This includes many primitive African and Asiatic arboreal monkeys and a series of forms leading structurally to the baboons. The primitive types are short faced, but the baboons have a long muzzle associated with the vegetable diet and the correlated long tooth row. There are well-developed cheek pouches for the stowing-away of food, while the stomach (in contrast to the other subfamily) is simple.

The genus *Cercopithecus* includes most of the African monkeys commonly found in zoölogical gardens (as the green monkey, vervet monkey, and Diana monkey). Typical arboreal forms with a short face, they probably stand near the base of the monkey stock. The macaques (*Macacus*) are monkeys of fairly large size and mostly Asiatic in distribution but with a representative—the Barbary "ape" in northern Africa and Gibraltar; there are fossil forms from the Pliocene of Eurasia. The tooth row is considerably elongated, and the snout consequently projecting. These forms are only partially arboreal, some species living in great measure on the ground. From this, several intermediate types lead to the baboons (*Papio*). These forms have become completely terrestrial, with a four-footed plantigrade gait. The tooth row of these exclusively herbivorous types is much elongated, and a doglike muzzle is developed. The tail is short and in some of the related types may be practically absent. Baboons are found in the Pleistocene of northern Africa and Asia.

The second subfamily of the modern Old World monkeys is the Semnopithecinae, a comparatively small group including *Semnopithecus*, the langurs, and their relatives (mostly Asiatic, with one African genus). There is never any facial elongation, the body is slim, the hind legs especially long, the tail usually well developed. Instead of cheek pouches, there is a complicated stomach for food storage. Cross-crests on the molars are highly developed. All the members of the group are good arboreal types. Remains of ancestral forms are widespread in the Pliocene of the Old World; *Mesopithecus* (Figs. 270, *A;* 271) is known from the complete skeleton.

Manlike apes.—The Old World monkeys just considered constitute two specialized lines, neither of which can be considered as ancestral to the anthropoid apes or man. To follow the history of these higher types we must return again to the Lower Oligocene beds of Egypt, in which was found *Propliopithecus* (Figs. 267, *D;* 270, *C*), the oldest definitely identifiable member of this group of highly developed primates. Here again we have only a jaw to deal with, but, again, one that is quite characteristic. It is not more than an inch and a half in length, indicating a form much smaller than any living manlike ape. The lower molars are definitely five-cusped, in agreement with the great apes and in contrast with the living monkeys, and the jaw has the relatively great depth of the higher forms.

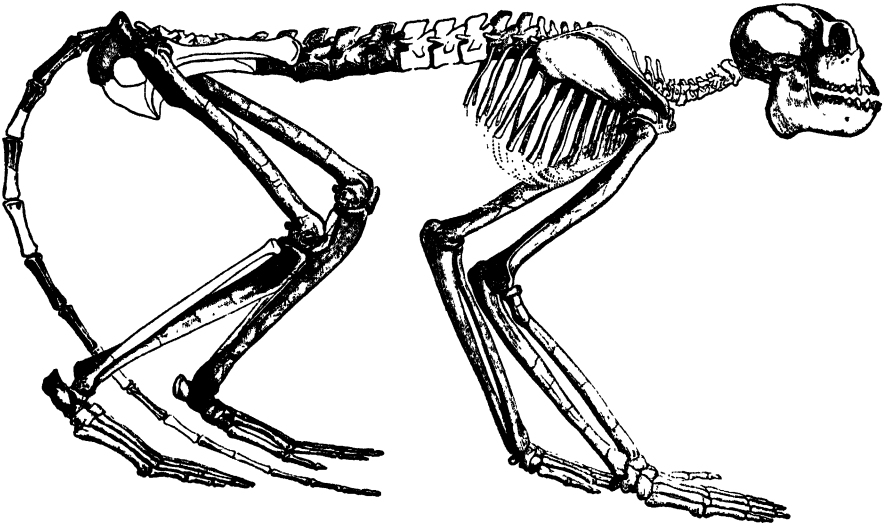


FIG. 271.—*Mesopithecus*, a Pliocene relative of the living langurs. About $\frac{1}{3}$ natural size. (From Gaudry.)

The family Simiidae, of which this is the earliest representative, includes four living types: the gibbon, the orangutan, the chimpanzee, and the gorilla. They are of large size, ranging from the comparatively small gibbon to gorillas several times as heavy as a man. In the quadrangular molars a fifth cusp (hypoconulid) is well developed below, while in the upper teeth the hypocone is comparatively small, the old trigon still being apparent. The molars tend to be rather long, and there is some lengthening of the face. The skeleton is rather close to the human type. The chest is broad in contrast to that of the monkeys; the ilia tend to broaden, as in man. The hands are rather similar to those of man, but the fingers are very long as compared with the thumb, and the arms much lengthened. The legs, on the contrary, are short; and the hallux, as well as the remaining toes, is much better developed and more finger-like than in man. These skeletal characteristics have seemingly developed in relation to the anthropoid-ape type of locomotion. With increasing size, normal four-footed progression in the trees has become increasingly impossible; and the members of the group normally progress by swinging from bough to bough with the body suspended from the hands. The feet are used more than ever as grasping organs and have so much lost their primitive mammalian character that most great apes cannot walk flat on their soles but must support their weight on the outer side of the foot.

It will be noted that in swinging by the arms the body is necessarily erect. Further, the front legs of all forms being much longer than the hind legs, the body is necessarily tilted up considerably in front in quadrupedal progression. Bipedal locomotion has thus begun among the arboreal types.

The brain is large, especially in the gorilla. But in these large forms its growth, as might be expected, has hardly kept up with the increasing body weight. Since the braincase is comparatively small, sagittal and occipital crests may develop, and the upper margins of the orbits project in most forms as supraorbital ridges above the front edge of the braincase. There is, as in most mammals, no projecting chin, the jaw sloping away under the symphysis.

Gibbons.—Smallest and most primitive of the living anthropoids are the gibbons (*Hylobates*) of the Malay region. The average gibbon stands about 3 feet high in the erect position. Alone among the living anthropoids, he customarily walks erect with the arms used as balancers. The gibbon, however, is almost entirely a tree dweller and with his long arms, which can reach the ground in erect position, is a very clever acrobat. The bulk of the gibbon brain averages about 90 cubic centimeters. This seems a small figure compared with that of man but is far above the average for a mammal of that size. The braincase of the gibbon is practically smooth, and the supraorbital ridges small. Vestigial ischial callosities are still present.

Pliopithecus, of the late Miocene and Pliocene of the Old World, was very similar to the living gibbon in almost all known respects; and from this, in turn, it is a short step back to *Propliopithecus*, from which it is generally agreed that the gibbon is derived.

Orangutan.—The orangutan, *Simia* (or *Pongo*), the "man of the woods" of Sumatra and Borneo, stands next above the gibbon in the scale of living primates. Considerably larger in size (adult males reaching nearly 5 feet), the orang is still a true arboreal type and is but a clumsy four-footed per former on the ground; the arms are somewhat shorter, reaching only to the ankles. The brain here is vastly larger than that of the gibbon, reaching 550 cubic centimeters in capacity. The braincase is expanded, crests rarely develop, and the supraorbital ridges are negligible. The tooth row, however, is long and the snout projecting, with a characteristic concave lateral profile to the face. Orang-like teeth are known from the Pliocene of India.

Higher anthropoid apes.—The highest living members of the anthropoid group are the chimpanzee (*Anthropopithecus* or *Pan*) and the *Gorilla*, both inhabitants of tropical Africa. It is generally agreed that these two forms are closely related. Both are less pronounced in their arboreal adaptations than the lower apes and monkeys; the gorillas spend much of their time on the ground, although walking as quadrupeds rather than as bipeds. Both are large, the chimpanzee exceeding 5 feet in height and old male gorillas more than 6 feet, with a weight of 600 pounds. The arms are short as compared with those of the lower anthropoids. Those of the chimpanzee reach a bit below the knee and those of the gorilla not quite so far. The brain is large in both, that of the gorilla having in some cases a capacity of 500–600 cubic centimeters, or at least half that found in some human races. Nevertheless, sagittal and occipital crests and supraorbital ridges tend to develop, being especially heavy in the old male gorillas. Associated with the long tooth row, there is considerable development of a muzzle. The canines are enlarged, and the dental arcade is U-shaped with the molars in two parallel rows, in contrast with the hyperbolic tooth row of man. Among interesting details in which these forms agree with man is the absence of the centrale in the hand, a bone otherwise almost universally present in the order.

In the late Miocene of Europe and Africa and the Pliocene of Europe and southern Asia there are a considerable number of specimens seemingly representative of the higher anthropoids but for the most part of somewhat smaller size than the living chimpanzee or gorilla. Unfortunately, all are fragmentary; and even in the best-known form, *Dryopithecus* (Figs. 266, *C;* 267, *E*), we have little more than the upper cheek teeth and most of the lower jaw. These creatures were certainly anthropoid apes and not men, for the canines, where known, are enlarged and the dental arcade has the ape U-shape. Their characters, as far as known, would permit of their being ancestral to the chimpanzee and gorilla, and very probably they are close to the human line as well. It is to be hoped that future discoveries may yield further and more adequate remains of these forms, so interesting because of their possible relation to our own phylogeny.

Australopithecus.—A number of ape finds from South Africa are from Pleistocene cave deposits. They show features approaching man more closely than any other of the manlike forms but are too late in time to be considered as actual human ancestors. The original find of *Australopithecus* (Fig. 270, *D*) was the skull of an infant. Discounting the fact that young apes resemble the human type more closely than does the adult, the skull exhibited various characters approaching the human condition, although the animal was clearly to be considered as ape rather than as man. This conclusion has been justified by the later finding of several fragmentary specimens of adult apes which are close to, if not identical with, *Australopithecus*. The general skull contours are definitely simian, but the brain capacity, estimated at 650 cubic centimeters in one instance, is rather above the maximum for existing apes, and in the rounded tooth row and reduced canines the dentition is close to the human pattern.

Giant ape-men.—In recent years there have been found fragmentary jaws of giant primates from the early Pleistocene of Java and southern China. The remains show features indicating that these animals (*Meganthropus*, *Gigantopithecus*) were close to the ape-human boundary and quite possibly primitive hominids. It would appear that nature "experimented" with gigantism in the human stock, as she did with many other types of animals in the Pleistocene.

Human characters.—Man and his close fossil relatives are usually placed in a separate family; but, as a matter of fact, the anatomical features which distinguish men from apes are comparatively few, although, from our own point of view, important. Of great significance has been the growth of the brain. The average European male has a brain capacity of about 1,500 cubic centimeters—much more than twice that of any of the great apes. This increase is mainly in the neopallium, the "gray matter" of the cerebral hemispheres. Here new centers are developed, such as those having to do with speech; and especially prominent are areas, absent in the apes, which seem to be the seat of higher human faculties. This enlargement of the brain results in a much expanded braincase and the consequent disappearance of crests and supraorbital ridges. In lower primates the prominent canines form a marked angle in the tooth row; in man the tooth row (Figs. 266, *D;* 267, *F*) is shorter and rounded, with the canines much reduced. In relation to this reduction of the tooth row, the face is less projecting, although there is a tendency in modern man for the retention of a long jaw in the development of a chin. With reduction of the face in general, the nasal region tends to develop into an isolated projecting structure.

Other important differences are associated with the change in locomotor habits. Even among the higher apes we have seen a trend toward terrestrial life; man lives on the ground as a biped. Man's arms are short compared with those of the apes; his legs, long. It is not probable that we have descended from such a long-armed, short-legged form as the orang but rather that, starting from a common ancestor with arms of rather indifferent length, the apes during millions of years of tree-living have elongated their arms to varying degrees, while man has retained more of the original proportions. The human hand, except for somewhat greater breadth and flexibility, is of a type probably present in the ancestral apes; the living great apes have tended to elongate the fingers, except the thumb, for hooking over limbs. A greater difference is in the foot. The usual primate foot is similar to the hand. This, however, is an awkward structure for ground life. In man the toes have greatly shortened, the hallux has lost its primitive opposability, and the calcaneum expands to form a prop at the back (the last is true of the higher anthropoid apes as well). In further adaptation to the bipedal gait, the back of man is much more sinuously curved than in the apes, with the effect of swinging the center of gravity up above the hips and raising the head.

The features listed above are among those which distinguish modern human types from the apes. Fossil human types tend to bridge this structural gap and exhibit intermediate conditions; but our knowledge of human ancestors is still a very imperfect one, and we know almost nothing of the evolution of the postcranial skeleton.

It is probable that the human line diverged from that of the great apes at about the *Dryopithecus* stage, in late Miocene times. There are, however, no certain skeletal remains of man in the Pliocene; it is not until the early Pleistocene that we find man present and already branching out into a number of types.

Early human cultures.—Man is a maker and user of tools, and this trait may well have appeared early in his development. Flint is a material which appears to have found favor for tool-making because it is easily fractured and worked and yet is extremely hard. Flints, thought by some to have been used by manlike creatures, have been reported from Tertiary rocks. While such finds are of dubious nature, flints were certainly being worked in early Pleistocene times, and a series of human cultural stages, based primarily on stone implements, has been established for the Pleistocene of Europe and, less surely, for other areas of the Old World. In the Lower Pleistocene, covering essentially the first of the four advances of the European glaciers and the following interglacial stage, implements were very crude ("eoliths"), and the stage may be termed (1) the Pre-Paleolithic. No associated human remains are known. The Middle Pleistocene, covering the second and third ice advances and a lengthy intervening stage, is the time of (2) the Lower Paleolithic, the first accepted subdivision of the Old Stone Age. In much of the Old World this was the time of the use of the large hand ax or *coup de poing*, associated with Abbevillian (Chellean) and Acheulean cultures; in other parts of Europe and Asia the time was one of the use of simple chopping tools and flint flakes, such as may have been used by *Pithecanthropus* and the related Peking man. (3) The Middle Paleolithic is the time of the third interglacial stage and the early part of the final (Würm) glaciation of Europe. The dominant culture is that of the Mousterian, characterized by well-shaped flint flakes and often found associated with remains of Neanderthal man. At the end of the Würm glaciation there is in Europe a characteristic series of cultures—Aurignacian, Solutrean, and Magdalenian—which constitute (4) the Upper Paleolithic (related cultures are found in other areas). In addition to expertly made flakes, bone has become an important cultural material. These cultures are the work of our own species, *Homo sapiens*. To Recent times rather than to the Pleistocene (and hence beyond our province) are to be assigned later human cultures—the Mesolithic; the Neolithic, in which pottery, agriculture, and domestication of animals were added to domestic economy; and the Bronze and Iron Ages of historic times.

Early men of eastern Asia.—Most adequately known of early human types are the finds from Java and China customarily termed the "Java ape man" and "Peking man." *Pithecanthropus erectus* (Fig. 272, *A*) was first discovered half a century ago on the banks of a Javanese river near the little village of Trinil, associated with an abundant mammalian fauna of Middle Pleistocene date. The original find consisted merely of a skull cap, with which were more or less doubtfully associated a thigh bone, several teeth, and jaw material (from another locality). In recent years several other partial skulls and jaws have been found, so that the cranial anatomy is fairly well known. The braincase, including the forehead region, was extremely low, and the brow ridges over the orbits enormous. Further, the skull is rather narrow compared to its length, a feature common to most early human forms (skulls in which, as here, the breadth is 75 per cent or less of the length are termed dolichocephalic; short-headed types, with the figure over 80 per cent, are brachycephalic; intermediates are mesocephalic).

Endocranial casts suggest an essentially human type of brain, although a small one; the average figure for endocranial capacity of 890 cubic centimeters is far below that of any modern human type, although well above the highest of apes. In contrast with modern men, the face was projecting and broad, with a large (and probably flattened) nose. The teeth were in most respects of human type, but there is evidence suggesting that the males had somewhat enlarged canines. There was no chin projection. If the femur is properly associated, *P. erectus* (as his specific name would imply) had already assumed an upright posture.

During the last fifteen years a considerable number of skulls and jaws of a primitive human type have been recovered from Middle Pleistocene deposits at Choukoutien, near Peking, China (Fig. 272, *B*). Their study has revealed another early type of man, similar to *Pithecanthropus* in many respects. The only conspicuous difference lies in the fact that the average of four endocranial cavities measured is about 1,050 cubic centimeters in the

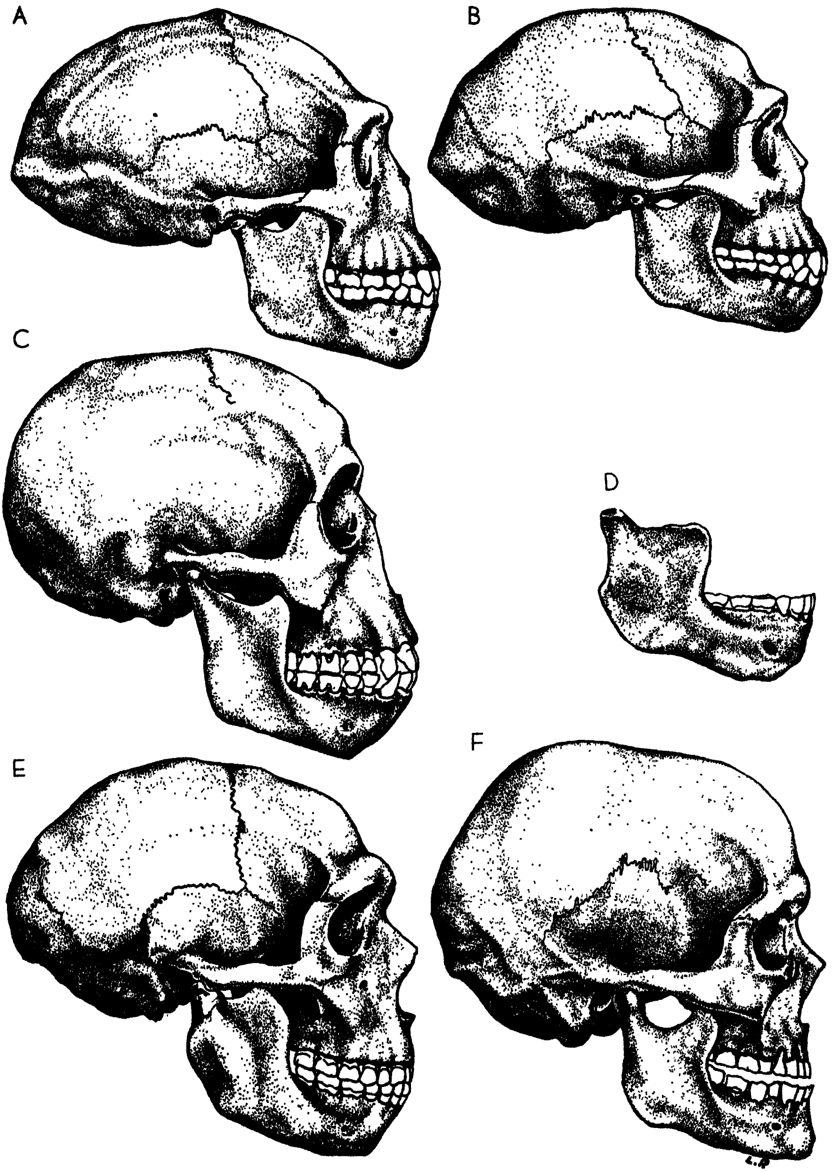


FIG. 272.—Skulls of fossil human types. *A*, *Pithecanthropus*, part of face restored; *B*, *Sinanthropus*, face and back part of jaw restored; *C*, *Eoanthropus*, face, some small areas of the braincase, and the tip of the jaw restored; the jaw doubtfully associated; *D*, the Heidelberg jaw; *E*, Neanderthal man; *F*, Cro-Magnon man from Grimaldi. (*A*, after McGregor and von Koenigswald; *B* after Weinert; *C* after, Elliott Smith; *E*, *F* after McGregor.)

Peking man, compared with a much lower figure in the case of the Java form. This is, however, thought to be due to the fact that the Chinese specimens may be for the most part males, the East Indian skulls measured those of females; sex differences in brain size are marked in many human races. The Chinese form was given a separate generic name as *Sinanthropus*, but students of these forms are currently agreed that they are closely related, if not specifically identical, races and that the general *Pithecanthropus* stock was a widespread early human type, in Asia at least.

Early European human finds.—*Pithecanthropus* is a primitive form, readily derivable from an advanced ape and, on the other hand, a good ancestor for Neanderthal man of the late Pleistocene. This suggests that early human evolution was a relatively simple and straightforward story. Finds from the early and Middle Pleistocene of Europe, however, complicate the picture.

The Heidelberg jaw, *Homo heidelbergensis* (Fig. 272, *D*), found in a sandpit not far from that German city, is perhaps our oldest human fossil, for it is from a deposit which is thought to pertain to the first interglacial stage, included in the Lower Pleistocene. Only the lower jaw is known. This is very massively built but, despite a few specializations, comparable to the general *Pithecanthropus* type, suggesting that relatives of this Asiatic genus may have been widespread in Eurasia.

Quite in contrast is the set of remains of *Eoanthropus* (Fig. 272, *C*), the "dawn man," discovered at Piltdown in Sussex in deposits which may be equally early. The type comes from a gravel bed which appears to have been laid down in the early Pleistocene but contains some redeposited Pliocene fossils. The whole skull and jaw were probably present originally in the gravel pit, but only broken pieces were recovered. There is, however, sufficient material to reconstruct everything except the facial region with considerable accuracy. The skull was highly vaulted, although thick-walled; the supraorbital ridges were nearly as weak as in a modern man; and the cranial capacity of 1,200 cubic centimeters brings it within the limits of our own species. In contrast with this, however, the jaw was very apelike, with a retreating chin, a canine which projected above the other teeth, and other features which have led some writers to believe that the jaw really did not belong to the skull but was that of a chimpanzee. There are, however, no Pleistocene fossil chimpanzees in Europe; and evidence for the association of jaw and skull is afforded by the discovery near by of a fragment of a second skull similar to the first, together with a tooth like those in the original jaw.

If the association is correct, early human evolution must have followed more than one path, for here the skull is far more advanced than in the roughly contemporary Asiatic pithecanthropoids, the jaw much less progressive. And even if the jaw be denied, we must seemingly admit that a contemporary of the low-browed *Pithecanthropus* had precociously developed a braincase much more advanced and comparable to that of modern man.

There are several other finds from the Middle Pleistocene of Europe (such as those at Swanscombe and Galley Hill in the lower Thames Valley) which tend to corroborate this evidence of a man with a modern type of skull vault in Middle Pleistocene times. However, these finds are either of a very fragmentary sort or of a questionable age, and the general picture of early human evolution in Europe is currently a blurred and confusing one.

Neanderthal man.—The characteristic human type of the Mousterian cultural period of the last interglacial stage and the early portion of the final European glaciation is *Homo neanderthalensis* (Figs. 266, *D;* 267, *F;* 272, *E;* 273), named from a German site but now known from a great number of localities in Europe and even represented in western Asia and northern Africa. The braincase had as high a cranial capacity as most living men (averaging about 1,550 cubic centimeters for males). This was mostly accounted for by the expansion in the occipital region of the brain, for the forehead was low and the supraorbital ridges greatly developed. These features, together with a face more elongate than in modern men and the undeveloped chin, must have given the creature in life a very apelike appearance. Here, for the first time, complete skeletal remains are known. The body was slightly stooped, the knees always slightly bent, and in other details (despite the relatively late date) there is still much suggestion of the creature's ape ancestors.

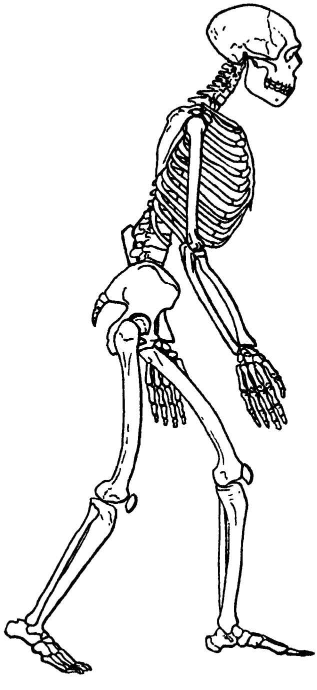


FIG. 273.—Skeleton of Neanderthal man. (After Weinert's *Ursprung der Menschheit* [Stuttgart: Ferdinand Enke].)

Modern man.—As the last glaciation drew to a close in Europe, there appeared a new series of cultures, the Upper Paleolithic—Aurignacian followed briefly by the Solutrean and Magdalenian. In these stages bone was used to a considerable extent; and the men of the time possessed a high degree of artistic talent, shown in the mural engravings and paintings of rock shelters.

At this comparatively late date (not more than 20,000 years ago at the outside) we find, for the first time in Europe, a modern type of man unquestionably to be assigned to our own species, *H. sapiens*. In such a race as the Cro-Magnon type (Fig. 272, *F*), associated with the Aurignacian culture, the forehead was high, the cranial capacity about 1,500 cubic centimeters, the supraorbital ridges gone, the face short, the nose well developed, and the chin protruding.

This sudden appearance in Europe of modern man, fully formed, raises difficult problems as to his origin. Some have believed that he was evolved from his European predecessor, the typical neanderthaloid. But there are few evidences of transitional features in European fossil men, and the cultural sequence suggests replacement rather than transition. It is probable that in Europe *H. sapiens* replaced and eliminated Neanderthal man.

Two other hypotheses remain. One suggests that the modern human type has no connection of any sort with the *Pithecanthropus-Sinanthropus* group or its Neanderthal descendants but has evolved independently throughout the Pleistocene, with *Eoanthropus* as an early representative. This is possible but, at present, is supported by little positive evidence. Still a third theory, halfway between the two extremes, suggests that *H. sapiens* has descended from some extra-European neanderthaloid and, after evolving to modern human standards, entered Europe as a successor to the related but comparatively unprogressive *H. neanderthalensis* then in possession.

Recently discovered neanderthaloid skeletons from Mount Carmel in Palestine show an admixture of modern characteristics. These individuals may be cited as evidence of an evolutionary progression from one species to the other, but they have also been interpreted as hybrids between the two species. The problem of the origin of modern man is still far from a solution.

Extra-European late Pleistocene types.—Our story of human evolution in the late Pleistocene has been told mainly on the basis of European discoveries. This is merely because this region has been more carefully studied than other sections of the Old World; the other portions of Eurasia and Africa have, as yet, been little explored but are beginning to yield many interesting finds.

At Broken Hill, Rhodesia, a skull from a cave deposit of an unknown but possibly late Pleistocene date is that of a man of bestial appearance, with a massive face, heavy brow ridges, and low forehead, suggesting Neanderthal affinities. It is thought that Rhodesian man may be related, through other archaic types from South Africa, to the ancestry of the living Bushmen.

Somewhat similar is *Homo soloensis*, represented by numerous partial skulls from the late Pleistocene of the Solo River in Java. This man, it is suggested, may be descended from *Pithecanthropus* and represent a stage somewhat below the typical neanderthaloid level. It is also thought that Solo man may be related to the ancestry of the Australians; other skulls from Java and Australia are interpreted as transitional in type.

Upper Paleolithic races of man which are apparently not too dissimilar to those of this age in Europe are known from areas as far removed from one another as Algeria, eastern Africa, and China. Several African finds which appear to be of some antiquity show primitive negroid features, and skeletons from the Upper Paleolithic of Grimaldi on the Riviera also show negroid characteristics. We have, however, no evidence as to the early history of the mongoloid type of man now dominant in eastern Asia.

The time of arrival of man in America has been a question of some interest. There is here no series of cultures comparable to those of the Old World, and no skeletons have been discovered which show marked differences from the modern Indian. Very probably man reached America only during or after the last retreat of the glaciers. But his arrival must have occurred at an early postglacial date, for finds in southwestern United States and in South America show that he was present at a time when ground sloths, horses, camels, and other types now extinct were still in existence in the Western Hemisphere.

CHAPTER 19

CARNIVORES

AMONG the varied mammalian groups which arose at the dawn of the Cenozoic, none is more prominent or more clearly derivable from the primitive placental stock than the order Carnivora, the flesh-eating mammals. The development of carnivores is a logical consequence of the insectivorous habits of the ancestral mammals. Once herbivorous mammals had come into existence, it was only to be expected that certain of the early insectivores should tend to prey upon them and take on various adaptations better fitting them for a flesh-eating existence.

Carnivore adaptations.—Modifications for this type of life markedly affect the dentition. A good set of incisors for biting off flesh and a pair of piercing canines are essentials which were already present in insectivores and are seldom modified in carnivores. The primitively sharp-cusped cheek teeth may undergo various changes. For flesh-eating, some sort of shearing apparatus to slice off the meat and cut tough sinews is a necessity. In insectivores there is some shearing effect between the back edge of each upper cheek tooth and the front edge of the following lower one (cf. Fig. 242). The carnivores have generally tended to emphasize the shear between a pair of highly specialized teeth called the carnassials. In the development of the opposed shearing surfaces, the originally diagonal line of meeting between the teeth tends to swing around to a fore-and-aft position, and the teeth concerned tend to simplify in structure and become high, narrow, and elongated. In different carnivore groups the pair of teeth which developed into carnassials has varied. In living types it is always the last premolar above, the first molar below; but in some early types the pair selected was $\frac{M^1}{M_2}$, in others $\frac{M^2}{M_3}$. Some forms never developed carnassial teeth, and others have lost them functionally in correlation with changes in diet.

The teeth behind the carnassials tend to be reduced and lost in the more purely carnivorous types. In forms which have a mixed diet they are less reduced and in some cases have become low-crowned crushing teeth capable of dealing with nuts, fruit, and the like.

A carnivore normally uses its claws for seizing its prey, and consequently there is but rarely any tendency to develop hoofs. The metacarpals and metatarsals are never greatly elongate, nor is there much reduction in the toes except for the pollex and hallux. Some carnivores (like the wolves) are rather good running forms; others (like the cats) depend upon a rapid dash and bound to obtain their prey. Many carnivores are more or less arboreal in habits, while some types have become aquatic forms. The clavicle is reduced or absent in carnivores.

We may picture a primitive carnivore as a small and perhaps arboreal animal much like the opossum in its general habits. In relation to arboreal life, pollex and hallux were somewhat opposable; there was a five-toed, semiplantigrade foot, and flexible limbs and body. The teeth would have been of the primitive tribosphenic type, with small shearing surfaces developing between neighboring molar teeth. The skull was presumably long, the brain small. These conditions are approached in some of the known early carnivores.

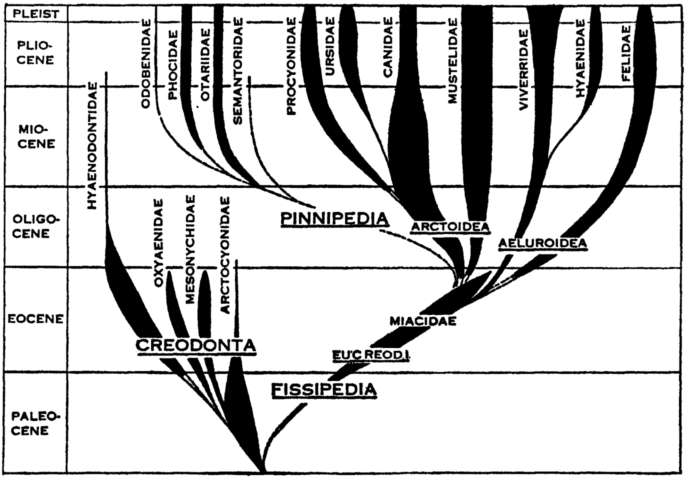


FIG. 274.—The phylogeny of the Carnivora

The general history of the group (Fig. 274) includes: (1) the early development of a group of primitive carnivores (suborder Creodonta) which flourished during the Paleocene and Eocene; (2) the radiation, at the end of the Eocene, from one early family, of the modern land carnivores (suborder Fissipedia); (3) the comparatively late development of marine carnivores (suborder Pinnipedia).

Creodonts.—The creodonts were the earliest and most primitive of carnivores. Appearing at the beginning of the Paleocene, they were very numerous throughout Eocene times. But with the disappearance of the more archaic ungulates upon which most of them presumably preyed, they rapidly dwindled in importance and in the Oligocene were almost entirely replaced by the more advanced fissipedes.

The creodonts were, in general, rather archaic in their build, and their characteristics were mainly negative, primitive ones. The skull was generally rather long and low; the braincase was small, with consequently well-developed sagittal and occipital crests. The dentition was usually complete, although exceptionally a small first premolar or the last molar might be lost. The molars were primitively tribosphenic; but there was considerable variation, especially in the development of carnassials. These sometimes remained undeveloped or, if present, occurred posterior to the position found in the fissipedes. In contrast with typical fissipedes, the auditory bulla was unossified; and in the carpus the scaphoid, lunar, and centrale were distinct. There was usually no loss of toes. The claws were usually either fissured or flattened and rather hooflike (Fig. 277, *A*). In habits there appears to have been considerable variation: some were probably omnivorous, some small types perhaps still mainly insectivorous, others may have been carrion- or mollusk-feeders, rather than typical carnivores.

The brain of the creodonts was generally of small size and their intelligence presumably low. This may have been a main cause of the early extinction of the group; for with replacement of the slow-footed and stupid herbivores of early Tertiary time by the swifter modernized ungulates, intelligent group pursuit (as in the wolf pack) or clever stalking (as in the case of the cats) became necessary for the capture of prey.

The creodonts, as here defined, may be divided into three infraordinal groups: (1) Procreodi, primitive types without specialized carnassials; (2) Acreodi, forms without carnassials but with heavy crushing teeth; (3) Pseudocreodi, typical creodonts with carnassials $\frac{M^1}{M_2}$ or $\frac{M^2}{M_3}$.

Primitive creodonts.—Most primitive of carnivores were the early members of the Procreodi, all of which are included in the family Arctocyonidae. These were abundant in the Paleocene. Many were of small size, with sharp-cusped cheek teeth in which no particular pair was set apart for shearing purposes. Primitive in many other characters, with very small brains, slim bodies, and slender limbs with sharp-clawed feet, they seem unquestionably to represent forms transitional from the primitive Cretaceous insectivores to later carnivores.

Primitive members of the family, such as *Oxyclaenus* and *Tricentes* (Fig. 275, *A*), were numerous in the Paleocene; few are found later, although one or two obscure carnivores in the Oligocene of Asia may represent survivors. Within the family there were several divergent lines. Some include forms of large size, such as the European *Arctocyon* and the American *Claenodon;* these grew as large as bears and were an early parallel to the bears in denti-

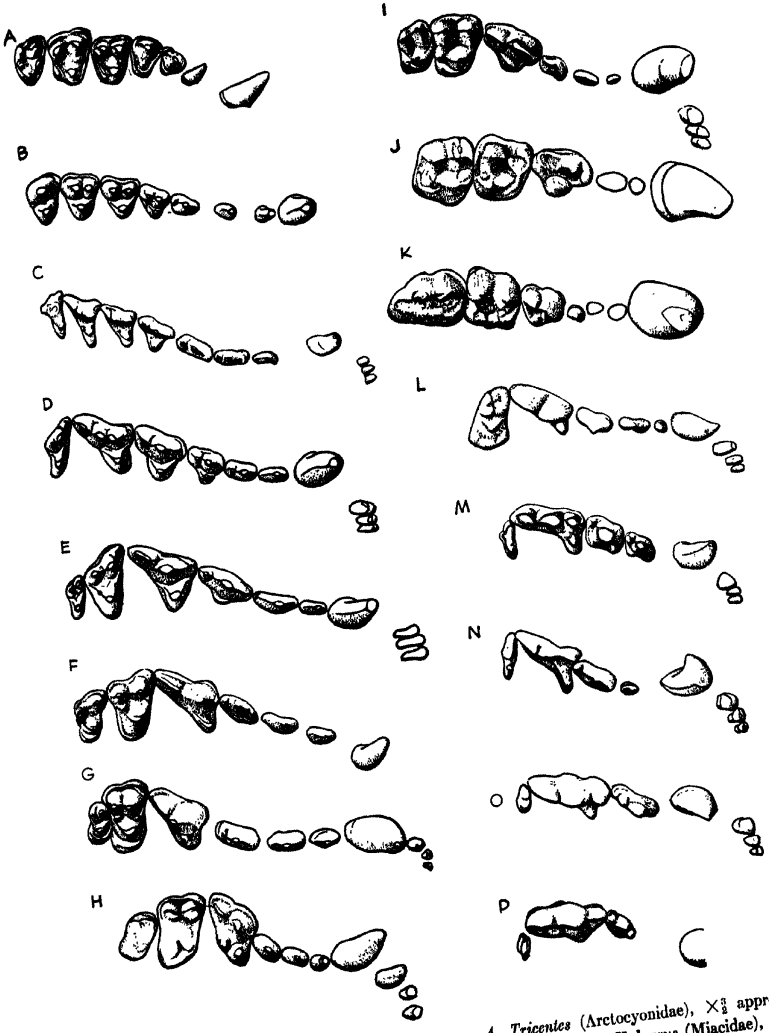


FIG. 275.—Right upper dentition of carnivores. *A*, *Tricentes* (Arctocyonidae), $\times\frac{3}{2}$ approx.; *B*, *Mesonyx*, $\times\frac{1}{2}$; *C*, *Sinopa* (Hyaenodontidae), $\times\frac{5}{8}$; *D*, *Oxyaena*, $\times\frac{1}{2}$; *E*, *Vulpavus* (Miacidae), $\times\frac{3}{4}$; *F*, *Pseudocynodictis*, a primitive fissipede, ×1 approx.; *G*, *Temnocyon* (Canidae), $\times\frac{1}{3}$ approx.; *H*, *Phlaocyon*, a primitive procyonid, $\times\frac{3}{4}$; *I*, *Hemicyon*, intermediate between dogs and bears, $\times\frac{1}{2}$; *J*, *Hyaenarctos*, a primitive bear, $\times\frac{3}{8}$; *K*, *Arctotherium*, a Pleistocene bear, $\times\frac{5}{12}$; *L*, *Mustela palaeosinensis* (Pliocene, China), $\times\frac{3}{8}$; *M*, *Hyaena bosei*, from the late Tertiary of India, $\times\frac{5}{12}$; *N*, *Dinictis*, an Oligocene true cat, $\times\frac{3}{4}$; *O*, *Metailurus*, a Pliocene true cat, $\times\frac{3}{4}$; *P*, *Smilodon*, a Pleistocene saber-tooth, $\times\frac{3}{8}$. (*A*, *B*, *G*, *H*, *M*, *N*, *P* after Matthew; *C–E* after Wortman; *F* after Scott; *I* after Gaudry; *J* after Frick; *K* after Merriam and Stock; *L*, *O* after Zdansky.)

tion and probably in omnivorous habits as well. Still others, including *Triisodon*, appear to represent the ancestors of the mesonychids.

Blunt-toothed creodonts.—The procreodonts were the characteristic carnivores of the Paleocene; the Acreodi and Pseudocreodi, descended from them, replace them in the Eocene. The Acreodi, including only the Mesonychidae, is the less important of the two, but the mesonychids are of interest because of their specializations and large size. In this family the upper cheek teeth were triangular, with blunt cusps; the lower molars had curious shearing talonids. The feet (Fig. 277, *A*) were wolflike in proportions but with flattened, fissured, distal phalanges which appear to have borne small hoofs rather than claws. *Mesonyx* (Figs. 275, *B;* 276, *B*) of the Middle Eocene had a skull a foot in length; later Eocene types grew to the size of a Kadiak bear, and the Mongolian *Andrewsarchus* had a skull a full yard long. The habits of these grotesque forms are difficult to guess at; suggestions as to diet range from carrion to mussels.

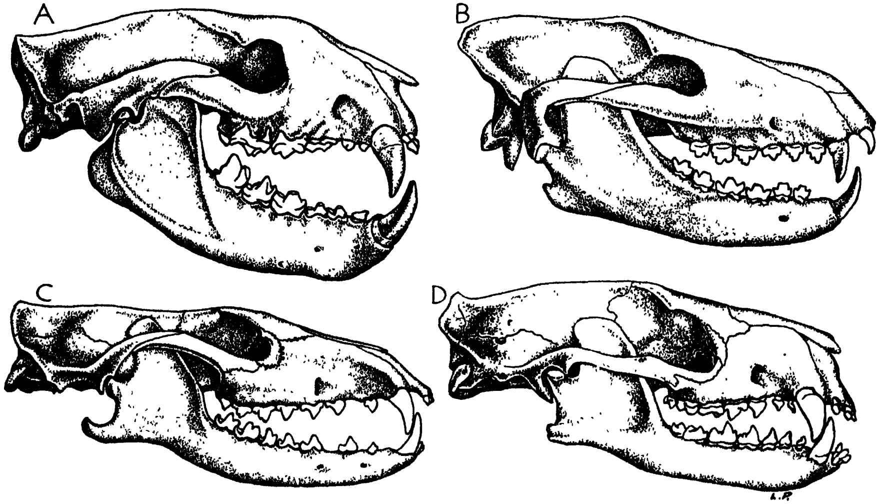


FIG. 276.—*A–C*, Skulls of early carnivores. *A*, *Oxyaena*, skull length 8¼ inches; *B*, *Mesonyx*, skull length 11 inches; *C*, *Sinopa* (Hyaenodontidae), skull length about 6 inches; *D*, the eucreodont *Vulpavus* (Miacidae), skull length about 3 inches. (*A*, *C* after Wortman; *B* after Scott; *D* after Matthew.)

Typical creodonts.—The characteristic carnivores of the true Eocene, the Pseudocreodi, belong to two families—the Hyaenodontidae and Oxyaenidae—both presumably derived from the Paleocene arctocyonids and both becoming progressively specialized to fit into the various modes of life afforded by the wide array of Eocene herbivorous types which formed their prey. In both families specialized shearing teeth were developed, as was the case in the miacids considered below, but farther back in the molar series; in further contrast with these forms, the claws of these typical creodonts were inserted into fissured terminal phalanges. The two pseudocreodont families are closely related and the taxonomic boundary between them is variably drawn.

The oxyaenids include a series of forms of the late Paleocene and Eocene. The skull was broad and short, the jaw deep and massive. $\frac{M^1}{M_2}$ developed as shearing teeth, and the postcarnassial molars tended to disappear. Typical members of the family were rather long-bodied, short-legged types with spreading plantigrade feet.

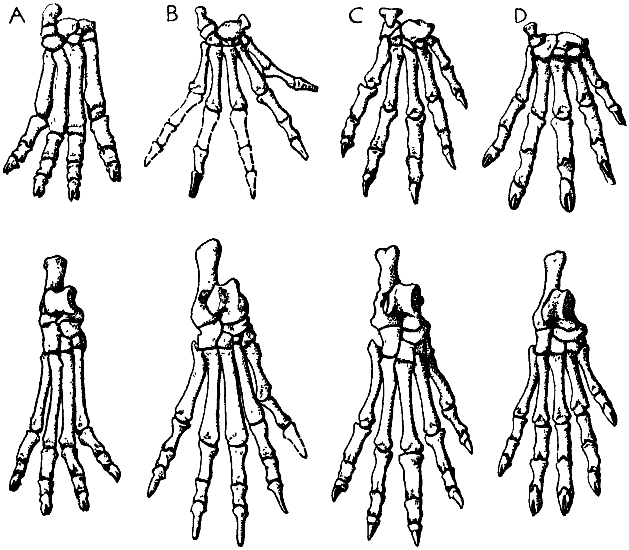


FIG. 277.—Feet of carnivores, manus above, pes below. *A*, *Synoplotherium*, a mesonychid creodont; *B*, miacids, manus of *Vulpavus*, pes of *Didymictis*; *C*, the Oligocene canid *Daphoenus*; *D*, *Hoplophoneus*, an Oligocene saber-tooth cat. (*A*, after Wortman; *B* after Matthew; *C* after Hatcher; *D*, after Adams.)

Although tending to grow to large size in some cases, they seem to have been somewhat comparable to the modern mustelids in habits. *Oxyaena* (Figs. 275, *D*; 276, *A*; 278), of the Lower Eocene, was a powerful wolverine-like animal which appears to be ancestral to the Middle Eocene *Patriofelis* of bearlike size and to *Sarkastodon* of the Upper Eocene of Asia, nearly as large as the contemporary *Andrewsarchus*. *Palaeonictis*, a rather catlike type from the Lower Eocene of both Europe and North America, is of interest in that the shearing function is shared by both M^1 and P^4 above, M_2 and M_1 below; it is thus structurally intermediate between the oxyaenids and the miacid ancestors of the fissipedes, although not ancestral to the latter.

A much larger assemblage is that of the Hyaenodontidae, a group which also appeared in the late Paleocene but, unlike the oxyaenids, survived in the Old World tropics in diminished numbers until late Tertiary times. These were forms in which the skull and tooth row tended to be more elongate than in oxyaenids, the jaw more slender, the body more slimly built. The limbs were rather longer, the feet more digitigrade in posture, and the nature of the terminal phalanges suggests the presence of typical claws in contrast to the flatter tips of the short toes of oxyaenids.

Some Eocene forms, such as *Limnocyon*, have a rather broad skull and M^1 over M_2 functioning as carnassials, as in the oxyaenids; they are included here, since in other features they are closer to the typical hyaenodonts. With this group is to be associated *Apataelurus*, an Upper Eocene genus known from a jaw remarkably similar to the saber-toothed cats of later Tertiary epochs.

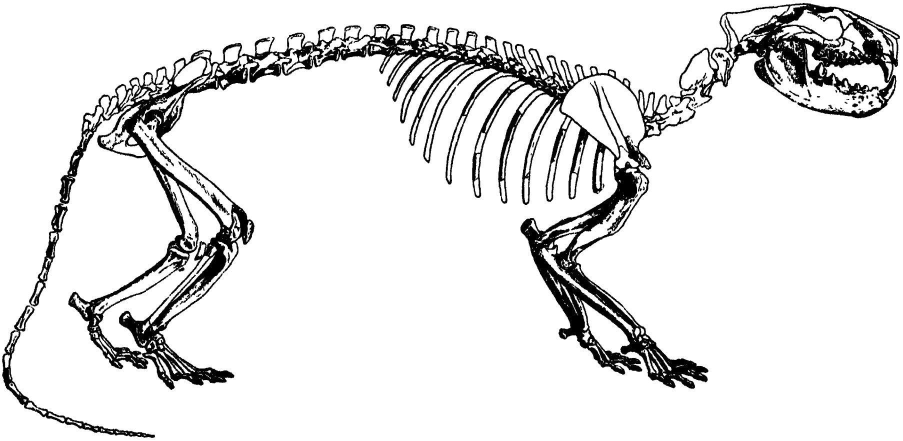


FIG. 278.—*Oxyaena*, an Eocene creodont (Oxyaenidae); original about 39 inches long. (From Wortman.)

More typical hyaenodonts are *Sinopa* (Figs. 275, *C*; 276, *C*) and *Hyaenodon*. These animals have long, narrow skulls and well-developed carnassials formed by M^1 and M_2. *Sinopa* of the Lower and Middle Eocene is representative of a series of small, lightly built genera; its species range in size from weasel to fox. *Hyaenodon*, found in both North America and the Old World in the Oligocene, was a much larger and more heavily built type which may have been able to prey upon the larger ungulates of the time.

These typical hyaenodonts form the exception to the rule that the creodonts did not outlast the Eocene. A considerable number of forms were still present in the Oligocene, and relatives of both *Sinopa* and *Hyaenodon* survived in the Old World tropics until Miocene and even Pliocene times.

The Miacids—fissipede beginnings.—The dominant carnivores of post-Eocene times were destined to come from another and relatively obscure group of Paleocene and Eocene animals—the Miacidae—which constitute the Eucreodi. *Didymictis*, the ancestral genus, appears in the Middle Paleocene, and the line is continued through the Eocene by *Miacis*, *Vulpavus* (Figs. 275, *E*; 276, *D*), and other genera. They are, for the most part, poorly known, for almost all were of small size; and there is considerable evidence that they were rather persistently arboreal forest dwellers—types which are infrequently fossilized. As in primitive carnivores generally, the body and tail were long, the limbs short but flexible, the pollex and hallux somewhat opposable (Fig. 277, *B*). The tympanic bulla was unossified, and there was no fusion of carpal bones. In such features they resemble the creodonts already considered; and the Eucreodi are very commonly grouped with the Creodonta in a horizontal type of classification. However, they differ from typical creodonts in a number of respects. The terminal phalanges are neither fissured nor flattened, as they are in creodonts. More significant, presumably, is the fact that the miacids are thought to have had relatively larger brain capacities than their creodont contemporaries; the rapid evolution of modernized ungulates may have placed a premium on brains as an important factor in survival. Finally, a diagnostic feature lies in the carnassial teeth. These were well developed and are formed, as in later fissipedes, by $\frac{P^4}{M_1}$. We shall here adopt a vertical classification and place the Eucreodi in the Fissipedia as a basal stock.

In late Eocene and early Oligocene days there began the development from the miacids of the diversified fissipede families which have since become the dominant land carnivores. The skeletal alterations necessary to transform a miacid into a typical fissipede are few—fusion of scaphoid, lunar, and centrale in the carpus into a single element and ossification of the auditory bulla—and these structures are seldom present in the fossil material (usually quite imperfect) of early fissipede genera. Deposits of the time of transition have yielded remains of a number of genera of small carnivores which are exceedingly difficult to place. They surely include the ancestors of later civets, weasels, and dogs; but these stocks were at the time almost impossible to separate, although there are slight but suggestive differences in the dentition. Were we living at the beginning of the Oligocene, we should probably consider all these small carnivores as members of a single family.

Cynodictis and *Pseudocynodictis* (Figs. 275, *F*; 282, *A*; 283) of the early Oligocene are typical primitive forms. The skeleton was much like that of a civet or a weasel. The body was long and flexible; the limbs short. All five toes were present on the short and spreading feet, which appear to have been armed with retractile claws. As in most later carnivores, the last upper molar had already disappeared. These genera are customarily considered primitive dogs, but in most respects they seem not far from ideal ancestors of the whole fissipede group.

Before the end of the Oligocene several of the major groups of carnivores had already become distinct, and by the latter part of the Tertiary the carnivores had become divided into the seven or more families still existing at the present time.

It has long been recognized that living fissipedes may be conveniently divided into two great groups; one, the Aeluroidea, includes civets, hyenas, and felids; the other, the Arctoidea, includes such types as dogs, raccoons, bears, and weasels. The fossils tend to support this division, although the distinctions are none too clear cut. The aeluroids, which we shall consider first, may be defined by such technical features as the fact that the tympanic bulla is (in contrast to the arctoids) a compound structure; the tympanic bone forms only the outer margin of the bulla, the remaining portion being formed by a separate ossification, the entotympanic.

Civets.—The basal stock of the aeluroids lies in the family Viverridae, including civets, genets, the mongoose, and a number of other Old World types. The civet, *Viverra*, is a representative form. It is a small carnivore with a long skull, a slim body, long tail, and short legs. All the premolars are present in this genus, but the first is tiny and is lost in many relatives. The carnassial is a good shearing tooth. Only two molars are present in either jaw; the upper ones are triangular and never develop a hypocone; the second is considerably smaller than the first.

In dentition and many other respects the typical civets are very similar to the ancestral miacids from which they are descended and from which early viverrids are difficult to distinguish; so similar are they that it has been suggested that miacids and viverrids might even be considered as constituting early and later members of a single, long-lived family.

The viverrids are characteristically the small carnivores of the Old World tropics. Small size, forest-dwelling habits, and tropical distribution all have tended to make them relatively rare in the fossil record; a number of genera are, nevertheless, recorded in Tertiary and Pleistocene deposits; none ever reached America. Despite the relatively primitive position of the family as a whole, the viverrids nevertheless show great variability in both fossil and recent genera. Among the variant types are some which are strikingly suggestive of the felid family. The existing fossa (*Cryptoprocta*) of Madagascar is a large and rather catlike viverrid; *Stenoplesictis* of the Oligocene is an ancient type showing similar specializations. By some writers these forms are considered as ancestral felids and placed in the Felidae. They are here, however, retained conservatively in the Viverridae; for, although they are structurally antecedent to the cats, it is doubtful whether they represent the actual viverrids from which the felids took their origin.

Hyenas.—A side branch of the civets which has progressed so far as to rank as an independent family is that constituting the Hyaenidae (Figs. 275, *M;* 282, *F*). The living hyenas of the Old World tropics are large scavengers with heavy and blunt teeth for bone-crushing. The carnassials are powerful, but of the postcarnassial teeth there remains only a tiny upper molar. The hyena is a digitigrade, running type which has lost hallux and pollex and has blunt nails rather than claws.

There are two living types—the striped hyena (*Hyaena*) of northern Africa and western Asia and the spotted hyena of South and central Africa (often considered as a separate genus, *Crocuta*); both were present in Europe in the late Pliocene and the Pleistocene. The hyenas can be traced back to the viverrids, from which they are a late offshoot. *Ictitherium* of the early Pliocene is intermediate in character, for, although trending in the hyena direction, it has the complete viverrid dentition and the teeth are not so heavy as in the modern types.

Conventionally grouped with this family is the "aard wolf," *Proteles,* of South Africa, which superficially has the appearance of a small, slim hyena. It is, however, an insect-eater, and in relation to this fact the jaws are (in marked contrast to the hyena type) slim in build and the teeth tiny and uniform in character. Like the hyenas the "earth wolf" is obviously a specialized offshoot of the civet group, but no connecting fossil forms are known.

Cats.—The most interesting of the aeluroids and in many ways the most specialized of all carnivores are the "cats," comprising the family Felidae. Almost all modern felids, from the domestic form to the lion and tiger, may be included in the genus *Felis* in a broad sense. In contrast to the dogs, for example, most cats, although digitigrade, are not good running types but depend for success in catching prey on a sudden leap onto their victim; the skeleton is hence more flexible than that of the dog, the claws are sharper and are retractile. The pollex is lost in modern forms, although the hallux is retained. The skull is comparatively short and high. The canines are powerful. The premolars partake somewhat of the carnassial pattern, and one upper and two lower ones are functional (there are one or two additional small ones in the upper jaw). The carnassials are well developed as purely shearing structures of two blades. The cats are almost pure carnivores, and there is no grinding surface left in their dental battery; as in the hyenas, only a tiny first upper molar remains behind the carnassials.

The living felids may be considered as typical of a subfamily, the Felinae. In sharp contrast are the extinct saber-toothed "cats," Machaerodontinae, of which the Pleistocene *Smilodon* (Figs. 275, *P;* 279, *B*) is a good example. In the saber-tooths the upper canines were exceedingly long stabbing and slicing structures; the lower canines were correspondingly reduced, and there was often a flange at the front end of the lower jaw serving as a guard for the upper canine tooth. Connected with this specialization were many related ones. The jaw was so constructed that it could be opened to about a right angle; the reduced ascending ramus of the jaw and the high-crested, V-shaped back part of the skull are related to the consequently changed position of the temporal muscle. The mastoid process was powerfully developed for the attachment of muscles which pull down the head. It is believed that the saber-tooths preyed mainly upon such thick-skinned animals as masto-

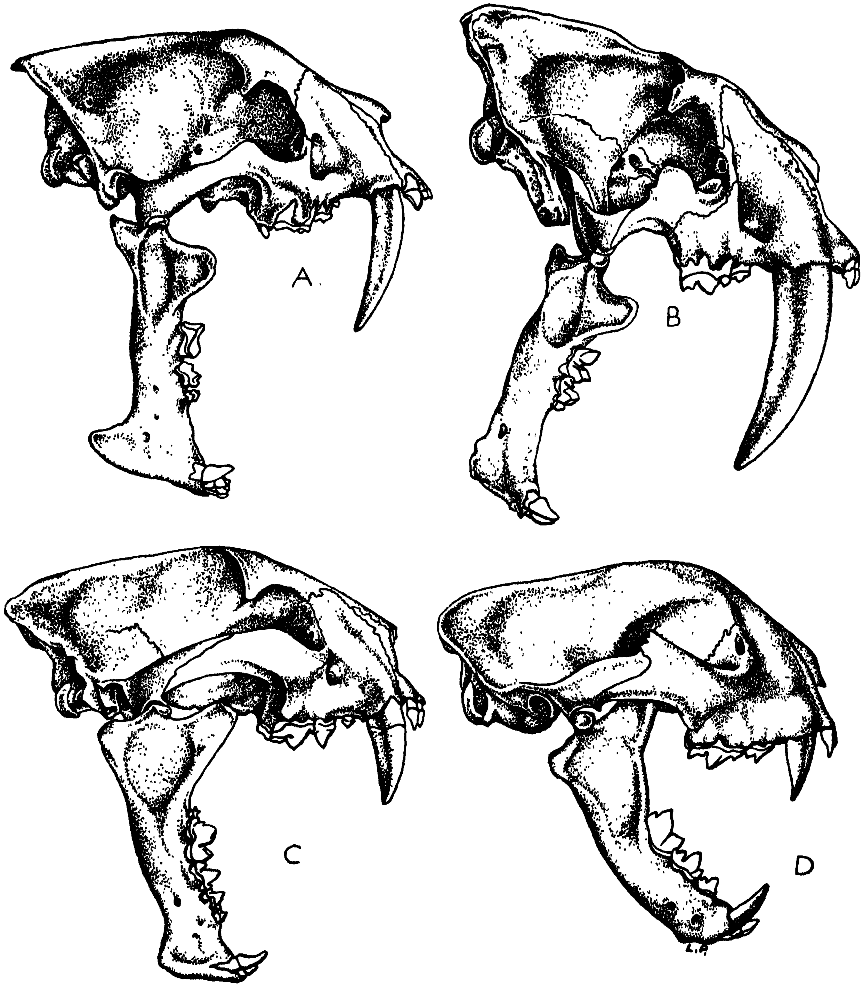


Fig. 279.—Skulls of saber-tooths and true cats. *A*, *Hoplophoncus*, an Oligocene saber-tooth, skull length about 6½ inches; *B*, *Smilodon*, Pleistocene, skull length about 12 inches; *C*, *Dinictis*, an Oligocene form with small sabers possibly ancestral to the true cats, skull length about 6¾ inches; *D*, *Metailurus minor*, a Pliocene true cat, skull length about 5¾ inches. (*A–C* after Matthew; *D* after Zdansky.)

dons and elephants; a deep stab would have been necessary to reach vital structures, and the sabers may also have been effective in slicing wounds which would cause death by copious bleeding.

The felids had the most rapid development of all the fissipede families. In the late Eocene and early Oligocene, at a time when, as we have said, most of the modern families could hardly be told from one another or from their miacid ancestors, we find that even highly specialized saber-tooths were already present. *Hoplophoneus* (Figs. 279, *A*), a characteristic American Oligocene form, shows all the essential characters of the later saber-tooths, although they were here not so highly developed; the skull was not so high posteriorly, the saber not quite so long (although the jaw flange was even more prominent), and the premolars were less reduced than in later forms. Saber-tooths were present at nearly every stage of the Tertiary in the northern continents; and in the Pleistocene they successfully "raided" South America, where the large native ungulates may have afforded an easy prey. Their eventual extinction may perhaps be associated with the increasing rarity of the large "pachyderms" upon which they preyed. It is possible that the mastodon was a favorite victim of the later saber-tooths. In North America these primitive proboscideans persisted until the end of Pleistocene times, and so did *Smilodon*. In Europe, however, mastodons disappeared at the beginning of the Ice Age, and the saber-tooths also disappeared early.

Modernized catlike types, *Felis* and related genera, with "normal" canines appeared in the early Pliocene. Their origin has been much debated, for all the better-known older felids have much larger canines and hence were saber-tooths of one sort or another. Those who believe that evolutionary trends never reverse themselves are forced to believe that the later felines have descended from earlier Tertiary ancestors who remained in obscurity in Oligocene and Miocene times and are not readily identifiable, if present at all, in the fossil record.

An alternative solution, however, has been suggested. Paralleling the typical saber-tooths from late Eocene to Pliocene, we find a series of forms which may be termed "false saber-tooths," of which the Oligocene *Dinictis* (Figs. 275, *N;* 279, *C;* 280) is typical. The upper canine was considerably larger than in modern cats, the lower canines small, and there was a distinct (although small) flange on the lower jaw. These false saber-tooths persist through the Miocene into the Pliocene. *Metailurus* (Figs. 275, *O;* 279, *D*) and *Pseudaelurus* of the Miocene and Pliocene belong to this series, but the jaw and dentition are less like the saber-tooths and closer to the living felines. It is thus not improbable that the "normal" modern cat tribe has evolved from saber-toothed ancestors.

Mustelids.—The arctoid group of modern carnivores, including weasels, dogs, raccoons, bears, and related types, may be distinguished from typical aeluroids by various technical characters. The claws, for example, are almost never retractile (as they are in the cats); the tympanic bulla is generally formed by the tympanic bone alone; there is a long canal running fore and aft beneath the bulla for the carotid artery, which supplies blood to the brain and skull region (cf. Fig. 239).

A basal group of arctoids, comparable in position to that of the viverrids among the aeluroids, is that of the family Mustelidae. The mustelids include such familiar forms as skunk, weasel, badger, wolverine, and otter. These are the characteristic small carnivores of the north temperate zone, parallel to the viverrids of tropical habitat. In general form and habits typical mustelids are, like the viverrids, relatively primitive. They tend to remain comparatively small in size, with short, stocky limbs and a full complement of toes; a majority have remained forest dwellers, and many are still more or less arboreal; almost universally the mustelids have remained good carnivorous types. Continued emphasis on a flesh-eating diet has not only resulted in the retention of well-developed shearing teeth in the greater number of mustelids but also in the reduction of the molars; no living mustelid has more than a single postcarnassial molar in either jaw. In most forms the upper molar has a characteristic expansion of the inner portion with a "waist" between the two halves. The reduction in the molars (and often in the anterior premolars as well) has been accompanied by a shortening of the facial region of the skull; seldom is any diastema developed.

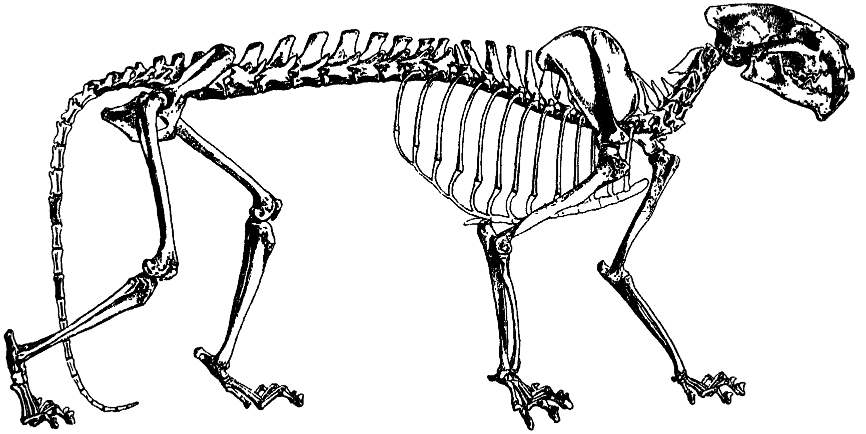


FIG. 280.—*Dinictis*, an Oligocene felid; original about 3½ feet long. (From Matthew.)

The taxonomy of the numerous modern forms is somewhat unsettled (some have proposed to divide them into as many as thirteen subfamilies); and the fossil history of mustelids is comparatively poorly known, for apparently most of them were forest-dwelling types.

The ancestral Oligocene forms were small, sharp-toothed carnivores. The two upper molars were usually still present, while the peculiar shape of the first molar had not been developed. These early types seem to have been very close to the more primitive dogs and even to the contemporary civet ancestors. The largest of all known mustelids is an early Miocene American form, *Megalictis*, somewhat comparable to a wolverine and as large as a black bear.

We may distinguish among later mustelids at least three main groups which appear to have been established before the close of the Miocene: (1) one including the weasels (*Mustela* [Figs. 275, *L;* 282, *E*]), martens, fishers, etc.; these are the typical small, short-limbed, bloodthirsty carnivores of the group and have retained a sharp, cutting type of dentition; (2) the wolverine (*Gulo*) and the "honey badger" of the Old World, large forms with robust teeth but predaceous habits; (3) a large group in which the dentition somewhat parallels the raccoons in that the carnassials have lost much of their shear while the molars tend to take on a grinding character; in many, insects are a prominent article of diet. The skunks (*Mephitis*, etc.) are the more generalized members of this group; the otters (*Lutra*, etc.) are related forms which have taken up an aquatic, fish-eating life, one even becoming a marine type, paralleling the seals; the badgers (*Taxidea*, etc.) are types in which the dentition is still less carnivorous, a hypocone being developed on the carnassial.

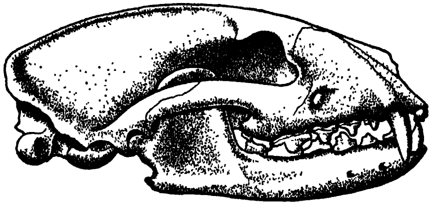


FIG. 281.—*Zodiolestes*, a Miocene procyonid, skull length about 4½ inches. (After Riggs.)

Dogs.—A second primitive arctoid stock is that of the family Canidae. Represented today by a considerable number of dogs, wolves, and foxes, the group goes back to the very beginning of fissipede history, and fossil types are very numerous, presumably because the canids have been in great measure dwellers in open-plains country. They are essentially cursorial terrestrial types with four digits well developed but with the pollex and hallux reduced, the toes close together, the claws blunt. The skull is long; the bulla typically large. The shearing function of the carnassials is well developed; but there is some grinding surface on the molars, two of which are normally retained above and two or even three below.

Cynodictis and *Pseudocynodictis*, described earlier, are among a series of small fissipedes which are very primitive in build but appear to lead to the dog group. Such forms appeared before the end of the Eocene. Early in the Oligocene there had evolved genera more definitely canid in nature. Half-a-hundred genera of doglike animals are known from the Tertiary, representing a complex series of phyletic lines. A main sequence appears to lead through such forms as *Cynodesmus* (Fig. 282, *C*) and *Temnocyon* (Fig. 275, *G*) toward the modern dogs, wolves, and jackals (*Canis*) and the foxes (*Vulpes, Urocyon*). In this line there was little tendency toward increase in size; the limbs were elongating, pollex and hallux were in process of reduction, and the running gait was evolving. Although now present in the three southern continents, canids were unkown in South America before the Pleistocene, and the

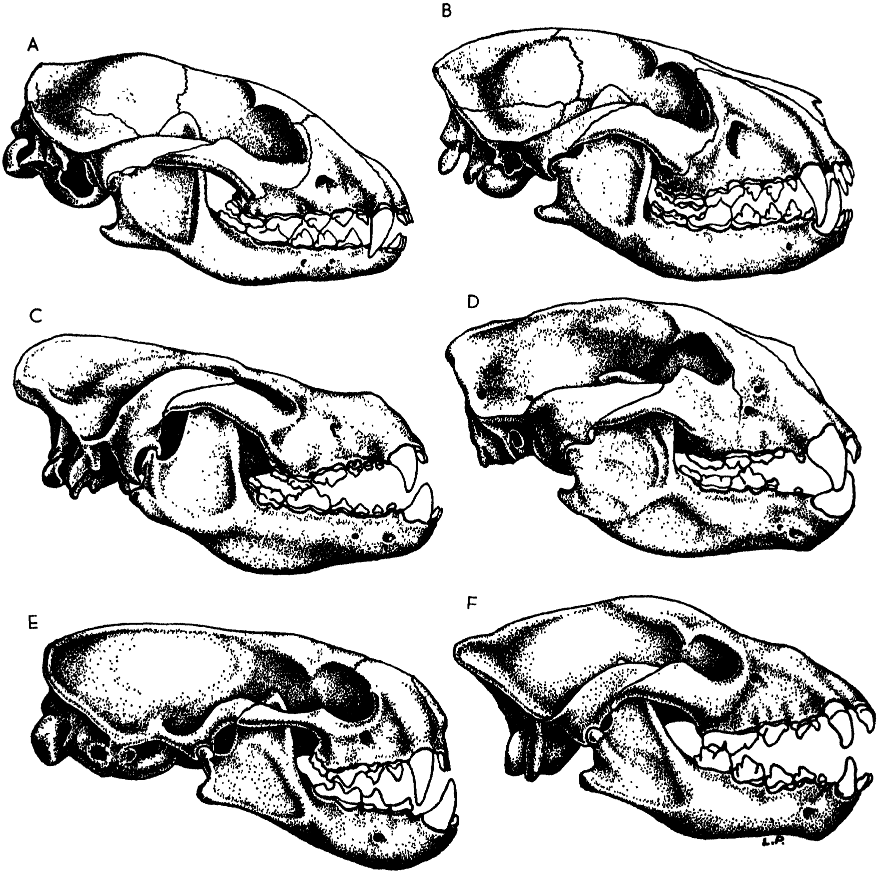


FIG. 282.—The skull in fissipede carnivores. *A*, *Pseudocynodictis*, a primitive Oligocene fissipede, length of original about 3¼ inches. *B*, *Cynodesmus*, a Miocene canid, length of original about 5¼ inches; *C*, *Hemicyon*, a Miocene form intermediate between dogs and bears, skull length about 13 inches; *D*, *Arctodus*, an American Pleistocene bear, skull length about 13 inches; *E*, *Mustela robusta*, an English Pleistocene weasel, skull length about 2⅜ inches; *F*, *Hyaena variabilis*, a late Tertiary fossil hyena from China, skull length about 9 inches. (*A* after Scott; *B* after Matthew; *C* after Frick; *D* after Merriam and Stock; *E* after Reynolds; *F* after Zdansky.)

dingo of Australia is quite possibly a type introduced by man. Dogs appear to have been the oldest animals domesticated by man, and remains of this camp-follower are common in Neolithic sites; probably the original dog was a wolf type, although the jackal has been advocated as an ancestor.

During the Oligocene there appears to have begun a second line leading to living types which include the dhole of India (*Cuon*), the African hunting dog (*Lycaon*), and the Brazilian bush dog (*Speothos*); a diagnostic feature is that the heel of the lower carnassial is merely a ridge rather than a basin as in other living types. *Otocyon*, the "large-eared fox" of South Africa, is of uncertain pedigree. This genus is of interest in that the number of molar teeth has secondarily increased so that there are often $\frac{4}{5}$ molars—one of the few cases in which the primitive placental number of teeth has been exceeded.

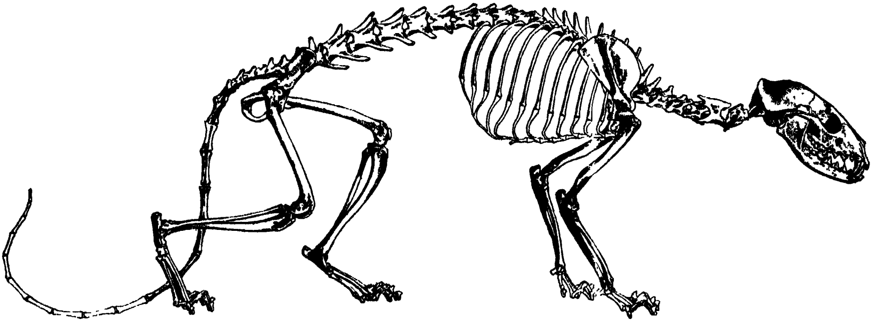


FIG. 283.—*Pseudocynodictis*, a small, primitive, Oligocene fissipede carnivore; original about 20 inches long. (From Matthew.)

There were a number of further lines of canid evolution which have failed to reach Recent times. One was a group of hyena-like dogs with peculiarly swollen foreheads, mainly American types of the Miocene and Pliocene (*Borophagus, Osteoborus*). In addition, there were several lines in which there was a tendency, in the Miocene particularly, for growth to considerable size and consequent ungainly form. Such canids are frequently termed "bear dogs." In the case of many genera, such as *Daphoenodon* (Fig. 284) and *Amphicyon* (which rivaled the bears in bulk), the term certainly is a misnomer, for, apart from size, there are few ursid features present; bears (and raccoons as well) are presumably descended from primitive canids, but not from this group. The build was heavy, the tail long and massive, the limbs short and powerful, the feet five-toed and rather spreading; unlike the bears, however, they were digitigrade types. The complete set of molars was retained and highly developed, while the shearing function of the carnassials was reduced. Obviously, these big forms were far from being pure carnivores.

Raccoons.—Fairly closely related to the canids are the Procyonidae (Figs. 275, *H;* 281), of which the raccoon, *Procyon*, is the type. This and most other members of the family are small, tree-living forms with semiplantigrade feet and a full complement of toes. The procyonids have a mixed diet; and, while there are only two molars, these have a good grinding surface. The carnassials have lost their shearing function, and the upper one has developed a hypocone. This obviously seems to be a reversion from the primitive carnivorous canid adaptations back toward an omnivorous diet. In other respects, however, the procyonids are seemingly merely a series of persistently primitive relicts of the arboreal ancestors of the dogs. There are several other forms from Central and South America, such as the kinkajou and the coati, which are customarily included in the Procyonidae. A bit further from the typical dogs is the true Asiatic panda, *Ailurus*, a somewhat larger terrestrial type with a better development of the grinding teeth. *Ailuropus* of Thibet is a still larger animal; this is the giant panda (frequently confused with the true panda), a large, bearlike creature with somewhat expanded molars. This form, however, is apparently not at all closely related to the true ursids, but simply an overgrown procyonid type.

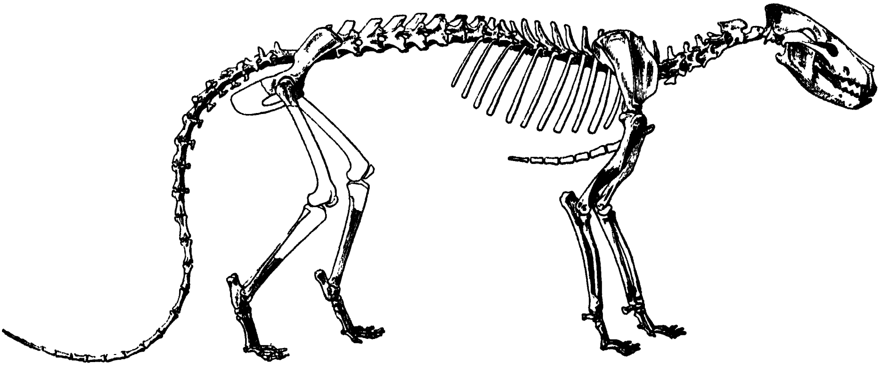


FIG. 284.—*Daphoenodon*, a Lower Miocene bear-dog; original about 5 feet long. (From Peterson.)

Phlaocyon (Fig. 275, *H*) of the Lower Miocene of North America is, perhaps, close to the ancestry of the raccoons. This animal was quite similar to the smaller dogs of the period except that the carnassial was losing its character with the development of the hypocone. The procyonids appear to have been primarily a North American group. Fossils are, however, rare, a fact to be associated with their usual arboreal habits. Members of the family reached South America in the late Pliocene as the first invaders of that continent from the north after its long Tertiary isolation.

Bears.—The bears, constituting the family Ursidae, are a further development of the arctoid "dog" group away from a carnivorous mode of life to a mixed and mainly herbivorous diet. Their ancestors had lost the last molar before giving up flesh-eating; but, in compensation, the remaining molars are much elongated, with a wrinkled grinding surface. Here, as in the raccoons, the carnassial has lost much of its shearing character, but no hypocone has developed, and the protocone has migrated backward. All the digits are retained in the plantigrade feet. While in diet and certain structural features the bears show some similarity to the raccoons, they differ in other characters, such as, for example, their notably large size, their generally terrestrial habits, and (as a minor feature) the stub tail. Presumably their similarities are due merely to the descent of both groups from the primitive dog stock of the Oligocene.

There are several distinct genera of modern bears. *Ursus* includes the large brown and grizzly bears; the black bears are sometimes separated as a distinct genus, *Euarctos*. These two groups are fairly similar structurally to each other and to *Thalarctos*, the polar bear. Certain forms from southern Asia, such as the Malay sun bear and the honey bear of India, are somewhat more distantly related; and the spectacled bear, *Tremarctos*, of South America, is a still wider departure from the common ursid type. Bears are not uncommon in the Pleistocene of Eurasia and North America: in Europe, *Ursus spelaeus*, a giant race of the brown bear, was a cave dweller contemporary with early man, while in the Americas short-faced relatives of the spectacled bear were present in both continents (*Tremarctotherium*, *Arctodus*, etc. [Figs. 275, *K*; 282, *D*]). It is agreed that the bears are of canid ancestry, but the exact line of descent is still subject to debate. The bears are the last of the arctoid families to appear; unquestioned ursids are unknown before the Pliocene. *Hyaenarctos* (Fig. 275, *J*) of the Pliocene was a large animal, with molars, as in bears, somewhat expanded. It is often regarded as a primitive bear but may be merely a canid parallel to the true ursids. *Hemicyon* (Figs. 275, *I*; 282, *C*) is a late Miocene form of moderately large size which is doglike in many respects; however, a significant feature is a backward migration of the protocone of the upper carnassial in bearlike fashion; this genus may well be a Miocene bear ancestor.

Pinnipeds.—A final subdivision of the order is that including the aquatic carnivores, the Pinnipedia. In the seals and walruses, in contrast with all other aquatic vertebrates, swimming is entirely accomplished by means of the limbs; in the seal ancestors, we may assume, the tail had been reduced, before aquatic habits evolved, to a slender, typically mammalian structure from which it was impossible to recreate a propulsive organ. The two hind legs in the seals have been turned backward to form a substitute for the tail, while the front legs are well-developed steering organs. In the limbs the upper segments are short and lie inside the surface of the trunk. The hand and foot are long, although there is no increase in the number of phalanges. All five toes are retained with webs of skin between them, the first digit often being quite strong and acting as a cutwater. Scaphoid, lunar, and centrale are fused in the hand, as in fissipedes (suggesting descent from that group). The dentition, for fish- or mollusk-eating, is regressive. The incisors tend to disappear, although the canines are usually well developed. The molars are usually reduced in number, but the premolars are preserved. There is no specialization of carnassials, and the cheek teeth form a uniform series of simple structure.

Most primitive in many ways are the eared seals (family Otariidae), in which group are included the fur seal and the sea lion. External ears are present, and the hind legs are still flexible enough to be brought around forward again from the swimming position for locomotion on land. The cheek teeth have but a single cusp and usually but a single root. The family goes back to Lower Miocene strata in which *Allodesmus* is a rather primitive type. Practically all known fossils are from the shores of the Pacific, which thus appears to have been the ancestral home of the family.

An offshoot of this group is *Odobenus*, the walrus of northern seas, placed in a distinct family. It appears to be structurally related to the eared seals but is larger and clumsier, earless, and with a dentition adapted to mollusk-eating. There are huge, rootless upper canines, but most of the other teeth are small and tend to drop out early, leaving a few heavy pegs of premolars for shell crushing. The oldest forms, such as *Prorosmarus*, of the Upper Miocene, were somewhat more primitive and closer to the eared seals.

The Phocidae, earless seals, are the most abundant pinnipeds today. These forms are more completely adapted for water-living; the hind legs cannot be turned forward at all. In contrast with the eared seals, however, the cheek teeth are usually two-rooted and have accessory cusps.

As with the two other types, the earless seals may be traced back to the Miocene. Beyond this date, however, our record of pinniped ancestry cannot be traced. It has been suggested that they have descended directly from Eocene creodonts. But a number of features suggest that they have been derived from primitive fissipedes, probably of the arctoid group.

In this connection a most interesting specimen is that of *Semantor* from the Lower Pliocene of western Siberia. Only the posterior part of the body is present; this shows a basic seal-like structure, particularly comparable with that of the phocids. But the limbs are more primitive; *Semantor* apparently was a shore dweller, able to walk on land to a fair degree as well as swim. Further, a long, slim tail was still present. Although too late in time to be an actual ancestor of the pinnipeds, *Semantor* may be a persistent survivor of an ancestral group. In a number of respects this primitive seal exhibits otter-like characters. Perhaps the seals have descended, like the otters, from early mustelids.

CHAPTER 20

ARCHAIC UNGULATE GROUPS

UNDER the head of "ungulates," or hoofed mammals, may be ranged almost all the larger herbivorous members of the class. The name, however, is not entirely a distinctive one; for while typical forms, such as the horse and cow, have hoofs, there are included in the ungulate orders a number of animals with well-developed claws and even such types as the purely aquatic sea cows. Nor do the ungulates form a single natural group, for the hoofed condition has undoubtedly been attained independently by various lines; and, strange as it may seem, a cow is, for example, probably as closely related to a lion as to a horse.

Despite the artificial nature of the assemblage, there are certain structural changes which have been generally undergone in the transformation of a primitive placental of whatsoever group into a large herbivore—changes having chiefly to do with dentition and the locomotor apparatus.

Ungulate teeth.—The generalized dentition of primitive placentals was unfitted for a purely herbivorous diet; low-crowned, sharp-cusped molars are not suitable organs for undertaking the thorough mastication which leaves, grain, or grass must undergo before passing into the digestive tract; and the development of a large grinding area is an obvious necessity for a herbivore. The primitively triangular upper molars have tended to square up, usually by the development of a hypocone at the back, giving essentially a four-cusped tooth in which the two intermediate conules have played a varying role (Fig. 241, *B*, etc.). In the lower molars the paraconid has disappeared, and the heel is built up to give a type of tooth with the talonid and trigonid of equal height, each contributing two of the four principal cusps—protoconid, metaconid, hypoconid, and entoconid.

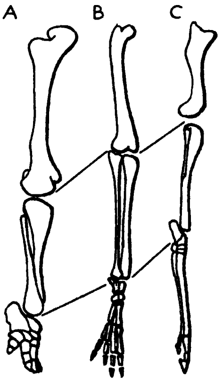
The originally sharp tubercles generally softened down to low swellings, giving a bunodont condition found in many early ungulates (Fig. 290, *A*, *B*, etc.) and still present in an exaggerated form in the swine. Further changes have taken place in most groups. There may be an elongation of the individual cusps into curved ridges, most characteristically seen in the selenodont (crescent-moon-shaped) pattern of many even-toed ungulates, such as camels, deer, and cattle (cf. Fig. 336, *A*, *B*, *C*, etc.). More common, however, has been the development of connections between adjacent cusps, forming varied patterns of ridges (lophs) on the tooth. In a lophodont upper molar (Fig. 243) three lophs are most common: (1) an ectoloph, forming the outer wall of the tooth, connecting paracone and metacone and often (if the styles external to the cusps develop) with a W-shaped contour; (2) a protoloph, including the protocone and protoconule; and (3) a metaloph, similarly formed from hypocone and metaconule. There are sometimes varied secondary connections of these crests, and in some cases additional spurs and ridges may develop. The cross-crests may develop but not the ectoloph (primitive proboscideans, etc.); conversely, only the ectoloph may develop, leaving isolated rounded cusps internally, a bunolophodont tooth (as in titanotheres, chalicotheres [Fig. 320, *G*, *H*]). In the lower teeth a common development has been the retention and emphasis of the two V's of the original triangular pattern (Fig. 321). These ridges undergo various modifications; they may become crescentic in shape or develop into two hook-shaped ridges which may eventually become two cross-lophs very similar to those sometimes found in the upper teeth.

Food-grinding, with the passage of one tooth across the surface of its opponent, implies considerable wear; this wear is greatly increased when an animal takes up highly abrasive silicious food, such as grass; further, increased size of the individual only squares the grinding surface available while cubing the amount of food required. It is not surprising, therefore, to find that, although many early types had low-crowned (brachyodont) molars, many ungulates develop a high-crowned, prism-shaped type of cheek tooth which will stand a very considerable amount of grinding before being worn down to the roots and exhausted.

In this process of development of hypsodont teeth we find that the cement, originally confined to the roots of the teeth, plays a prominent part. If nature were to construct a high-crowned tooth merely by greatly elongating the original ridges and cusps, the product would be a series of thin parallel columns, easily broken and full of crannies. One alternative "solution" would seem to be that of enormously thickening the block of dentine above the root, leaving the cusps as superficial structures. This, however, is seldom seen except in some archaic and comparatively unsuccessful mammals. Instead, in a number of groups, there has been a development of the cement so that it completely covers the tooth before eruption and fills all the interstices between the ridges. This results in a solid structure which, upon wear, exhibits all three tooth-forming substances on the crown—dentine in the center of the ridges, a hard enamel layer at their boundaries, and cement outside and filling all vacant spaces (Fig. 287).

Increased surface may also be attained by elongation of the row of grinding teeth. This may be accomplished by the increase in size of individual teeth, and in many cases (as in the horses) molars in later types are longer than in earlier ones. But a more common process by which this end has been attained is by expanding the premolars (usually of comparatively small size to begin with) and adding them functionally to the molar grinding series. Independently in a large number of groups may be traced a progressive increase in the surface area of the premolars, and in some cases (horses, for example) all except the first of these teeth have become almost identical in structure with the molars (cf. Fig. 320, *A*, *B*).

The cropping of food is the function of the anterior portion of the dentition. For this duty the incisors are commonly retained, as in the horse. But the upper ones may be lost (as in the cow), the upper lip or a horny pad taking their place; and we find here and there various other specializations, such as the much enlarged, chisel-like incisors of South American ungulates. The canines are often functionless and reduced or absent; and in most ungulate groups we find a gap, or diastema, developing between the front group of cropping teeth and the grinding series in the cheeks.



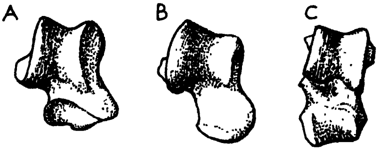


FIG. 286

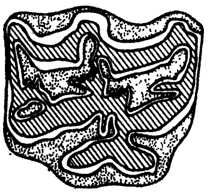


FIG. 285

FIG. 287

FIG. 285.—*Left*, hind limbs of elephant, opposum, and horse, to show changes in limb proportions from a primitive condition (*B*) to (*C*) that of a fast-running ungulate with short femur and long metapodials, and (*A*) a graviportal type with a long femur and short broad foot. (Mainly after Gregory.)

FIG. 286—*Upper right*, astragali of Eocene ungulates: *A*, *Heptodon*, a perissodactyl; *B*, *Phenacodus*, a condylarth; *C*, *Homacodon*, an artiodactyl. (*A*, *B* after Osborn; *C* after Marsh.)

FIG. 287.—*Lower right*, a worn upper molar of *Equus*, to show the arrangement of the three tooth materials—enamel (*unshaded*), dentine (*hatched*), and cement (*stippled*).

The ungulates have always been the main source of food for the larger contemporary flesh-eaters. In connection with defense, horns or hornlike structures have developed in many groups. Sometimes (especially in early types) there may be large stabbing canines. In general, however, the best defense is flight; and rapid locomotion, both for escape from enemies and for migration from one feeding ground to another, is characteristic of ungulates.

Ungulate limbs.—In the more typical ungulates the limbs are elongated and the limb bones usually slim. In fast-running forms the humerus and femur are relatively short, giving a speedy drive to the leg as a whole, while elongation of the second segment of the limb increases the scope of each stride. With this elongation there is often a tendency toward the reduction of the ulna and the fibula and the placing of the entire weight on radius or tibia. There is never, however, a complete loss of these bones, for they carry important muscle attachments and articulations, and the ends are usually present but fused with the remaining bone. There is practically no capability of rotating the limb segments; motion tends to be restricted to a highly efficient fore-and-aft drive. Most ungulates have an alternating type of carpus (and tarsus)—one, that is, in which the connections between the elements and with the metapodials are so arranged that each functional toe helps support at least two of the three proximal carpal elements. The astragalus (Fig. 286) usually develops a rounded and deeply grooved upper surface, over which the tibia glides without danger of turning or twisting.

The primitive placental was presumably more or less plantigrade. With faster locomotion, the metapodials (and thus the palm and sole) tend to be lifted off the ground, giving a digitigrade gait. With further development of speed the digits themselves are lifted, until the animal may touch the ground only with the tips of the toes—the unguligrade condition. With the result of attaining solid stance, hoofs are developed; the terminal phalanx of the toes broadens and is surrounded on the front and sides by a thick, nail-like modification of the original claw, while a horny layer padded by elastic tissues protects the flat lower surface.

With the lifting of the hand and foot into an unguligrade position, it is obvious that the shorter lateral toes would fail to reach the ground and would become nonfunctional. This was, in most groups, followed quite naturally by a reduction of these side toes and strengthening of the central ones. The hallux and pollex, which not only are short but originally diverged at an angle from the other toes, were the first to go. Beyond this stage reduction has taken place according to two schemes. In the majority of ungulates (as in the ancestors of the horses, for example) the third toe was the longest, and the axis of symmetry of the foot lies through this digit (mesaxonic). In such forms the fifth toe has usually been lost, giving a three-toed condition; and further emphasis of the central toe and reduction of lateral ones has led in the modern horses to the development of a one-toed form (Figs. 319, 328, 329). In other ungulates, such as the ancestors of the cow and pig, the third and fourth toes were primitively equal in length, and the axis of symmetry passed between them (the paraxonic type). As in mesaxonic ungulates, pollex and hallux usually disappear, and many forms are found to be in a four-toed state. Frequently, however, the two central toes have enlarged, and the lateral ones have dwindled or vanished, to leave a two-toed form; the cloven hoof of the cow or deer is, of course, really two appressed digits (Figs. 342, 348, 350).

Simultaneously with toe reduction, changes have usually occurred in the metapodials. In fast-running forms there has been a great lengthening of these elements, giving a third functional segment to the limb through which an additional upward and forward drive may be imparted to the body. With the reduction of the toes, metapodial reduction usually takes place as well. Splints of bone often represent the metapodials of lost digits, as in the horse; while, on the other hand, the metapodials may be incomplete, although small nonfunctional toes may remain as dew claws. In paraxonic forms the two main metapodials may fuse in advanced types into a single element—the cannon bone.

In typical ungulate running, the forward spring is given chiefly by the hind legs; the forelimbs bear the main impact on landing. The clavicle is usually absent, thus releasing the body from any solid connection with the front limbs and allowing the shock to be taken up by the elastic "give" of the muscles slinging the body between the shoulder blades.

The heavy ungulates, such as the elephants, have a different locomotor "problem" somewhat comparable with that of the dinosaurs. In an animal of this sort—the graviportal type—the limbs tend to be large straight columns, with the femur and humerus longer than the second segments (Fig. 285, *A*), giving a powerful, rather than a speedy, muscular action. There is little elongation of the metapodials, and all the digits tend to be retained to form a semicircular clump presumably inclosed, in fossil forms as in the living elephant, in a thick pad. The pelvis tends to be so shaped that the head of the femur lies beneath it rather than at the side, and the ilia are typically expanded laterally into broad wings in relation to the changed position of the muscles.

Ungulate classification.—The term "ungulate" covers, as we have noted, a vast and varied assemblage. Most living forms are included in two orders—the mesaxonic (odd-toed) perissodactyls and the paraxonic (even-toed) artiodactyls—which have flourished in the northern continents since the beginning of the Eocene, while the elephants, conies, and sea cows are surviving members of an ancient African group of subungulates. There are, in addition, a number of entirely extinct groups which will be treated in the present chapter.

Ungulates are unknown in any Cretaceous deposits but presumably must have been developing from the primitive placental stock at the very beginning of the Tertiary; for, by the end of the Paleocene, four distinct types of archaic ungulates were already present. These include: (1) the Condylarthra, a Paleocene and Eocene order which includes a number of generalized and primitive types and may be close to the ancestry of many later forms; (2) the Amblypoda, clumsy, archaic ungulates which had attained large size in the Paleocene but became extinct by Oligocene times; (3) the Dinocerata, a rather comparable group from the late Paleocene and Eocene; (4) the Notoungulata, rare and disappearing early in the northern regions but attaining a striking development in the Cenozoic of South America. This last continent, owing to its isolation, formed an area in which still other archaic groups survived through the Tertiary. These include: (5) the Astrapotheria, (6) the Litopterna, and (7) the Pyrotheria.

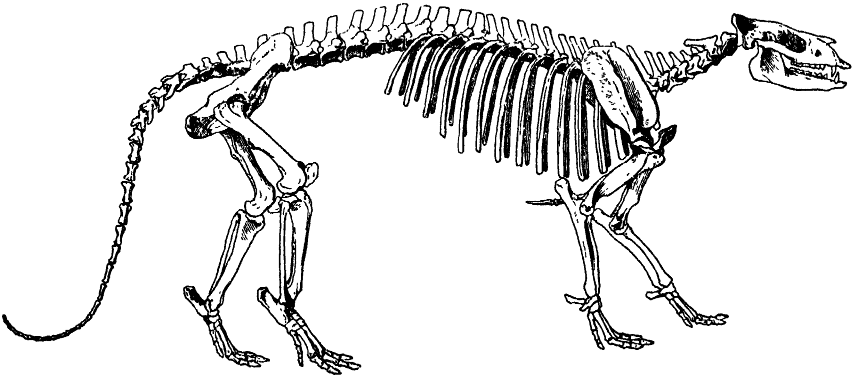


FIG. 288.—*Phenacodus*, a primitive ungulate (Condylarthra), original about 5½ feet long. (From Osborn.)

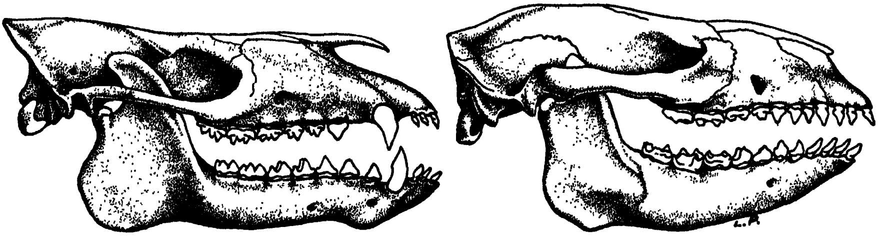


FIG. 289.—*Left*, skull of the condylarth, *Phenacodus*, length about 9 inches. (After Cope.) *Right*, skull of *Hyopsodus*, length about 2¾ inches. (After Matthew.)

Condylarths.—The order Condylarthra includes a number of Paleocene and Eocene ungulates of primitive character. Best known of the group is *Phenacodus* of the Lower Eocene of North America and Europe (Figs. 288; 289; 290, *A*, *B*; 291). This ungulate reached a size rather considerable for the times, the largest species attaining the dimensions of a tapir. Its general appearance was that of a carnivore rather than an ungulate, for the tail was long and the limbs short and quite primitive in structure. The radius and tibia were about the same length as humerus and femur, and ulna and fibula were unreduced. There was little elongation of the metapodials; and all five toes were present, although (in mesaxonic fashion) the third toe was somewhat the longest and strongest. The carpus was serial in nature, each distal element lying directly beneath a proximal one, without the sharing of support characteristic of the alternating type of ungulate carpus. The clavicle, however, had already disappeared; and one certain ungulate character was present in that there were obviously hoofs on the stumpy end-phalanges.

The skull, again, was much like that of the creodonts—long and low, with orbits open behind and with a sagittal crest in correlation with the very small brain. The dentition was complete, the canines were still large, and there was only a slight diastema. However, the cheek teeth were already partially adapted for a herbivorous, rather than a flesh-eating, mode of life. The molars were in the bunodont stage. Six cusps were present above and below, for a hypocone had already developed in the upper molars, while the paraconid was still present in the lower teeth. The premolars were still comparatively simple; the last lower one had attained a molar-like appearance, but none of the upper ones had passed beyond a tritubercular stage.

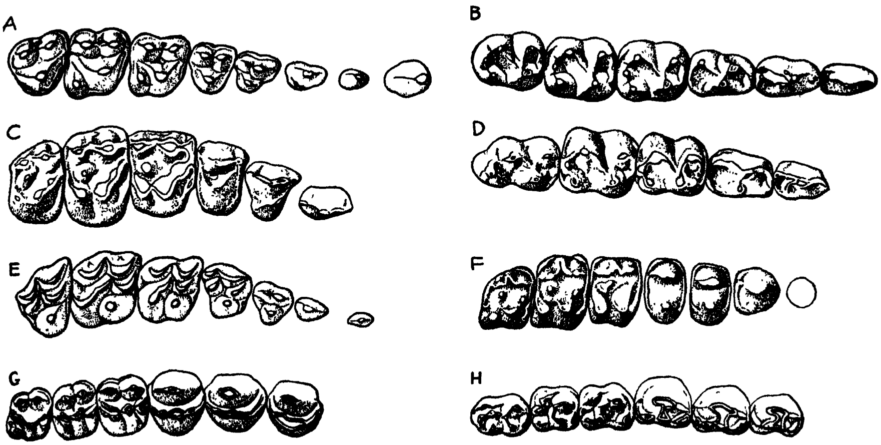


FIG. 290.—The cheek teeth of condylarths: *A*, *B*, right upper and left lower cheek teeth of the condylarth *Phenacodus*, $\times \frac{5}{6}$ approx.; *C*, *D*, same of *Hyopsodus*, $\times \frac{3}{2}$ approx.; *E*, right upper teeth of *Meniscotherium*, $\times \frac{5}{4}$ approx.; *F*, right upper teeth of *Didolodus*, a South American condylarth probably related to litoptern ancestry; *G*, *H*, right upper and lower left cheek teeth of *Periptychus*, $\times \frac{2}{3}$ approx. (*A–E*, *G*, *H* after Matthew; *F* after Ameghino.)

This interesting form was once believed by some to be the ancestor of the later ungulates, particularly the perissodactyls. But it is rather late in occurrence and much too large to occupy such an ancestral position, and some of its characters (as the serial carpus) are not those expected in an ancestor of the later groups. In the Paleocene of North America occurs *Tetraclaenodon*, which appears to have been a direct ancestor of *Phenacodus*. In this somewhat smaller form the dentition was more primitive in nature, and the feet were apparently terminated by rather broad claws instead of hoofs. *Ectocion*, of the late Paleocene and Lower Eocene, had teeth of a type similar to those of perissodactyls, although not itself an ancestor of the odd-toed forms.

Very different in many respects was *Hyopsodus* (Figs. 289; 290, *C*, *D*), a form about the size of a hedgehog which was common throughout the Eocene of North America. In skull and dentition *Hyopsodus* was rather primitive and not unlike certain insectivores or lemurs. There was no diastema; but the canine was reduced, and the teeth were of uniform height, while the molars were of the bunodont type of many primitive ungulates. Primitive, again, were the clawed phalanges and the short and spreading feet; it is not improbable that *Hyopsodus* was a semiarboreal type. Despite these facts, it is to be regarded as a condylarth rather than as an insectivore or primate, with which groups some would place it. *Mioclaenus* and its Paleocene relatives are mainly known from cheek teeth which are quite sharp cusped and similar to those of early creodonts.

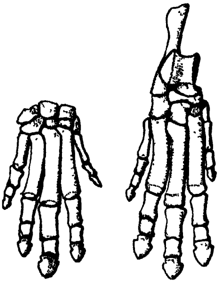


FIG. 291.—Manus and pes of *Phenacodus*, a Lower Eocene condylarth. (After Cope.)

Little *Meniscotherium* (Fig. 290, *E*), of the late Paleocene and Lower Eocene of North America, represents still another type of condylarth, with a peculiar combination of characters. The molars were advanced in structure, with a selenodont pattern. The limbs were short and stout, as in *Phenacodus;* but the feet (as in *Hyopsodus*) appear to have had clawlike structures rather than hoofs. The relationships of this odd form are none too clear. A connection with the Old World conies or some South American ungulates has been suggested.

Periptychus and a number of North American Paleocene allies form a family of archaic ungulates of uncertain ordinal position. *Periptychus* was nearly as large as *Phenacodus*, although occurring much earlier (in the Lower and Middle Paleocene), and, except for rather shorter limbs, would have had perhaps much the same general appearance in skull and skeleton. The premolars, however, were much enlarged, with heavy principal cusps, and in the molars extra cusps were added to the primitive pattern both above and below (Fig. 290, *G*, *H*). Smaller members of the family were also present.

It has long been suspected that the condylarths were ancestral to the litopterns of South America (discussed later in this chapter). Tending strongly to confirm this conclusion is the identification as condylarths of *Didolodus* (Fig. 290, *F*) and a number of other ungulate genera in the late Paleocene and Eocene of that continent. This is, to date, the only find of any characteristic northern group of placentals in the early Tertiary of South America.

It is obvious that in the condylarths we are dealing with a group of very primitive ungulates. In all of them, the teeth were distinctly adapted for a herbivorous diet, but their low-crowned and generally bunodont condition shows them to have been very primitive herbivores indeed. In the postcranial skeleton *Phenacodus* alone appears to have possessed true hoofs, but even in that form there were few other ungulate characteristics. It is not improbable that the more primitive condylarths (although not *Phenacodus*) were quite close to the stem of many of the later ungulate groups, but our present knowledge permits of no definite statement.

Amblypods.—A second group of archaic hoofed mammals which appeared in the Paleocene is that of the amblypods, earliest of ungulates to achieve large size. *Pantolambda* (Figs. 292, 293, 294) of the Middle and Upper Paleocene was the first of the order to appear. This was an animal about the size of a sheep, which, with its short limbs and short, broad feet, already merited the "slow-footed" name applied to the group, although the structure was as yet relatively primitive. The cheek teeth are of a simple pattern, the triangular upper molars with V-shaped cusps, the canines moderately large.

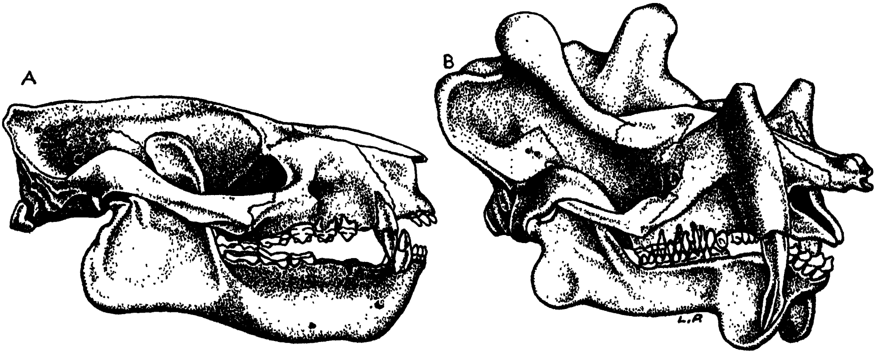


FIG. 292.—*A*, *Pantolambda bathmodon*, a Paleocene amblypod, skull about 6 inches long; *B*, *Uintatherium*, an Upper Eocene member of the Dinocerata, skull about 2½ feet in length. (*A* after Osborn; *B* after Marsh.)

In the late Paleocene and Lower Eocene the amblypods had increased greatly in size and had diversified to become a dominant group of large and ungainly ungulates. In the late Paleocene, *Sparactolambda* and *Barylambda* are well-known American genera. The former had grown to dimensions about two and a half times those of *Pantolambda*, with greatly developed canines and clawed rather than hoofed feet. This quite un-ungulate feature we shall see developed in other later groups of "hoofed" mammals and here, as elsewhere, it is believed to have been associated with root-eating. *Barylambda* was about 8 feet in length, with a short but high body, heavy limbs and tail, and a small skull, in which the canines were not particularly prominent.

In the Lower Eocene, *Coryphodon* (Figs. 293, 295) ranged widely from North America to Europe. This form was about the size of *Barylambda* but quite different in many respects, such as the rather longer body and the long, slender tail. The skull was large, with a broad muzzle, broad arches, and a flaring occipital region. The canines were large and the upper molars peculiarly developed. Paracone and metacone form a diagonal posterior crest, and the protocone develops into a parallel ridge anterior to this.

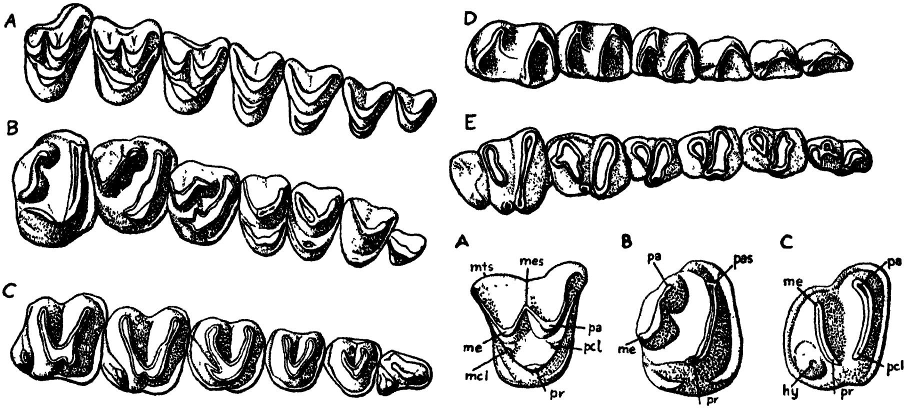


FIG. 293.—*Left*, right upper cheek teeth of amblypods and uintatheres. *A*, *Pantolambda*, about $\frac{3}{4}$ natural size; *B*, *Coryphodon*, about $\frac{1}{3}$ natural size; *C*, *Uintatherium*, about $\frac{5}{12}$ natural size. *Upper right*, *D*, left lower cheek teeth of *Coryphodon*, about $\frac{1}{3}$ natural size; *E*, same of *Uintatherium*, about $\frac{5}{12}$ natural size. (Mainly after Osborn.) *Lower right*, right upper molars of amblypods and uintatheres. *A*, the Paleocene *Pantolambda; B*, the Lower Eocene *Coryphodon; C*, the late Eocene *Uintatherium*. In *Pantolambda* the tooth is of a simple tritubercular pattern. The homologies in *B* and *C* are disputed; the interpretation here adopted is that of Simpson. For abbreviations see Figures 241, 322.

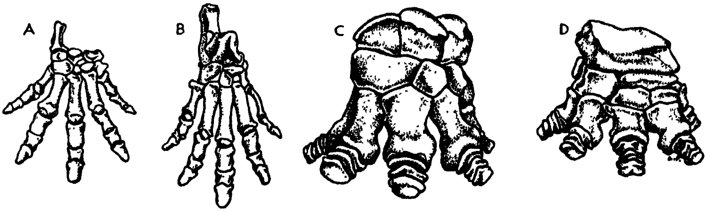


FIG. 294.—*A*, *B*, Manus and pes of the Paleocene *Pantolambda;* C, D, *Uintatherium* of the Upper Eocene. (*A*, *B* after Osborn; *C*, *D* after Marsh.)

This is the last appearance of amblypods in North America, but in Asia genera fairly close to *Coryphodon* survived into the late Eocene and Oligocene.

Uintatheres.—Still more grotesque than the amblypods were the uintatheres. These flourished especially in the later part of the Eocene of North America in such genera as *Uintatherium* (Figs. 292, 293, 294), which was as large as a modern African rhinoceros and was the giant of his day. In their ponderous build, short limbs and feet, and other weight-carrying adaptations, the uintatheres are similar to the amblypods and were once thought to belong to that group. There is, however, no evidence of relationship apart from these adaptive features, and the uintatheres are now considered to form a separate order, the Dinocerata. As the name implies, the characteristic genera have developed pairs of hornlike bony swellings above the long, low skull on nasals, maxillae, and parietals; and powerful upper canines were presumably additional weapons of defense in the males. The upper incisors were usually absent, the lower ones small. The upper molars were of peculiar construction, with two crests, converging internally, occupying most of the surface of the tooth. It is believed that one ridge is formed by protoconule and paracone, the other by protocone and metacone. This structure has no parallel in the true amblypods (or elsewhere) and indicates a long separate line of descent of the ungainly uintatheres from a primitive ungulate stock. Outside of North America, uintatheres are unknown except for *Gobiatherium* of the Asiatic Upper Eocene—a form with a very long, low skull which lacks the large upper canines of the American forms and has no horns except possibly some small nasal structures.

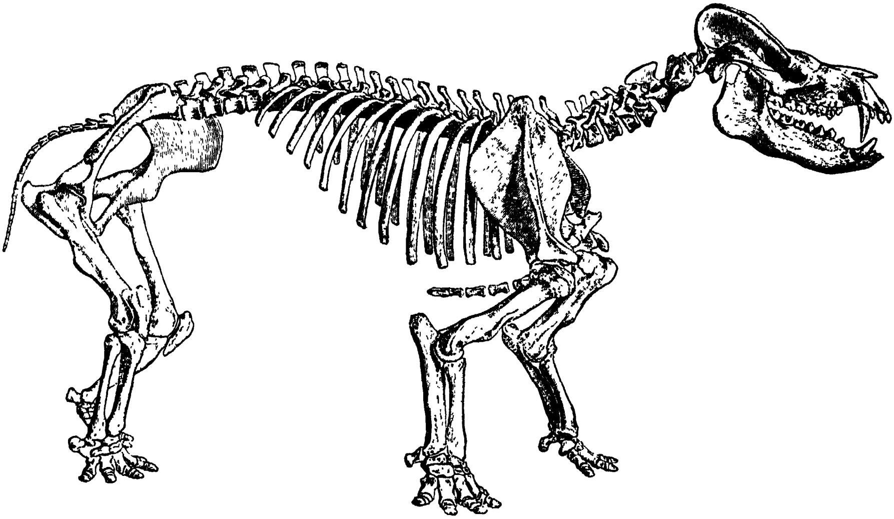


FIG. 295.—*Coryphodon*, a large Lower Eocene amblypod. Original about 8 feet long. (From Osborn.)

The oldest uintatheres are from the late Paleocene; forms of that age were somewhat more primitive in structure but, nevertheless, rather large and highly specialized animals. They are not represented in earlier American Paleocene deposits, and their origins are hence unknown.

South American ungulates.—The archaic ungulate groups so far considered were short-lived; by the Eocene, or Oligocene at the latest, they had disappeared in the Northern Hemisphere in the face of competition from more progressive ungulates and the presence of numerous enemies among the placental carnivores. For archaic types, however, South America offered a haven of refuge.

That South America was cut off from the other continents at a very early Tertiary date seems to be indicated by the fact that but few placental mammals appear to have been present at the time of severance of continental connections. In the Eocene deposits of that continent have been found (in addition to the marsupials previously discussed) only a few edentates and a number of primitive ungulates of types almost unknown in other regions of the world.

In the isolation of South America, free from the depredations of the true carnivores and free from the competition of other hoofed mammals, these ungulates developed into an amazing variety of forms. In proportions they ranged from the size of a rat to that of an elephant. Some simulated the rodents in appearance and habits; others were analogous to the hippopotamus and the rhinoceros; still others were remarkably similar to horses and elephants in structure. These types were extremely interesting and often bizarre. But our consideration of them is hampered by the fact that, in the absence of existing representatives, we lack both popular names and that mental picture of the living form which in most cases furnishes us with a good starting-point for the discussion of mammalian groups.

These ungulate groups reached the climax of their development in the Oligocene and Miocene; with the Pliocene and Pleistocene came the advent of the carnivores, to which they probably fell an easy prey, and of higher ungulate types, with which they could not successfully compete for pasturage. By the end of the Pleistocene this once extremely numerous assemblage had vanished entirely.

It has proved difficult to establish the age of the beds in which these South American forms are found, since they differ in their mammalian fauna so greatly from those in other parts of the world. By some early workers these deposits were supposed to be considerably earlier in date than is now believed to be the case. In consequence of that belief, it seemed that forms which simulated the horses, elephants, and various other groups appeared in that continent considerably earlier than did these types themselves in other regions. Mistaking these parallelisms for real relationships, a patriotic Argentinian, to whom we owe much of our knowledge of these forms, laid claim to the origin of many mammalian groups for South America, a viewpoint which is frequently reflected in the names given to the various genera and groups.

Notoungulates.—By far the greater number of forms from South America are included in the order Notoungulata. The members of this group varied much in size and adaptive features, but many general structural similarities run through the various subdivisions of the order. The skull was typically rather short, flattened above, with a broad braincase and forehead, the nasals broad, the nostrils usually terminal. The zygomatic arches were broad and heavy, and there was never a postorbital bar. In all notoungulates there are peculiar features of the auditory region not found in any other order. Relatively few notoungulates show any reduction in the dentition or the development of a diastema; and while there were often strong chisel-like incisors, the rest of the teeth formed a series in which there was often a gradual transition from the small canine to the molars. Primitively brachyodont, the cheek teeth (Fig. 300) in many lines tended to become high prisms, often with persistently growing roots. Even in the earliest forms there was seldom any trace of the bunodont stage through which the ancestral forms presumably passed, and lophodont types of teeth were rapidly developed. The upper molars were lophodont, primitively triangular but coming to resemble superficially those of a rhinoceros, with a straight ectoloph, a long protoloph running back from this at an angle, and a metaloph perpendicular to the end of the ectoloph. A characteristic and even diagnostic notoungulate tendency is that toward the development of accessory cusps in the central valley of the upper molars. These may form secondary ridges or cause the tooth, on wear, to have a pattern of nearly continuous dentine with but a few notches or hollows lined with enamel. In the lower molars there was considerable resemblance to the perissodactyls in the development of two typically crescentic ridges; the front one was usually much the smaller. The most characteristic feature of the notoungulate dentition is the fact that the entoconid primitively lay isolated inside the curve of the posterior crescent (Fig. 301).

Although there is great variation, the feet were essentially mesaxonic in structure in a majority of cases, the number of toes tending to reduce from five to three. But there was never any great acquisition of true ungulate characters in the feet and never an attainment of the unguligrade position. A number of types appear to have had hoofs, but claws were present in many cases; the feet in general rather resembled those of rodents or the hyrax.

Ancestral notoungulates: the Notioprogonia.—With two exceptions, notoungulates are unknown beyond the boundaries of South America. These exceptions, however, are among the oldest records of the group. A single tiny jaw records the presence of a notoungulate, *Arctostylops* (Fig. 301), in the Lower Eocene of North America. Still more curious is the fact that in the late Paleocene of Asia the commonest animal so far discovered is a notoungulate, *Palaeostylops*. These discoveries suggest an Old World origin for the notoungulates and a long migration trail to South America. They do not prove this point, however; they merely indicate that notoungulates were widespread at an early stage of the Tertiary. It is further possible, although equally unproved, that the notoungulates developed in South America and that these records represent an early and unsuccessful invasion of other areas from a southern base.

Small archaic notoungulates, such as *Notostylops*, related to these forms, are the commonest of Eocene types. Except for reduction of the anterior teeth in some instances, they show no marked specializations of any sort. The molars show a simple pattern. Except for a single diagonal accessory ridge in some forms (*cf.* Fig. 300, *C*), the upper molars are still essentially triangular lophodont types, with protoloph and metaloph connected medially. These early forms may well be regarded as members of a basal suborder, the Notioprogonia, ancestral to the remaining notoungulate groups.

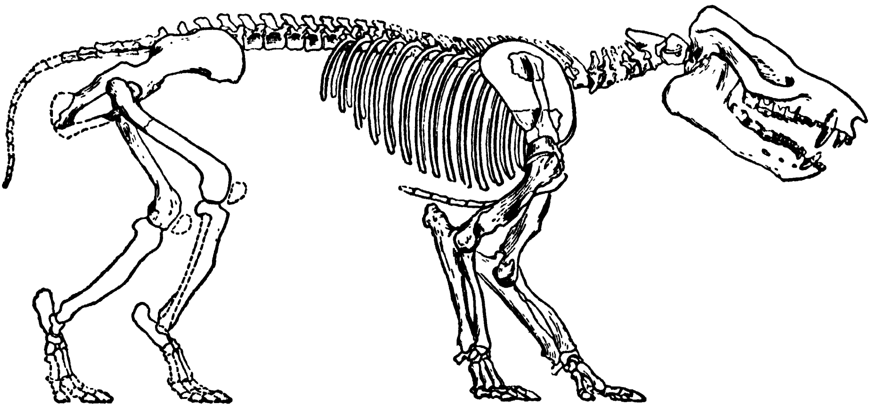


FIG. 296.—*Thomashuxleya*, a primitive Eocene notoungulate, about 5 feet long. (From Simpson.)

The skeleton is imperfectly known in these primitive forms; however, *Thomashuxleya* (Fig. 296), while technically ranged in one of the more advanced groups of notoungulates, is an Eocene genus which shows a general structure apparently primitive for the order and retained in many of the less specialized later types. The build is that of a rather slow-moving, and essentially digitigrade type, analogous to that of the amblypods and Dinocerata of northern continents.

Toxodonts.—The largest and most conspicuous of later notoungulates are the toxodonts. Typical toxodonts were present in the Oligocene, flourished greatly in the Miocene, and survived into Pleistocene times; the later genera were large, heavily built forms. Among the ungulate features of the skeleton may be mentioned the presence of but three hoofed toes on each foot and the absence of the clavicle (retained in some other notoungulates, however). But the ulna and fibula were always complete and heavy, although the latter sometimes fused with the tibia.

The teeth remained in a nearly closed row, seldom developing a diastema; and there was little loss except that the canines were weak or absent. The incisors were often expanded into chisel-like cropping structures, while the primitively low-crowned molars tended to become high crowned and rootless and sometimes were covered by a cement sheath. The upper molars curved in strongly toward each other, a feature to which the term "toxodont" (bow-tooth) refers; in surface view they are characteristically triangular, ectoloph and protoloph meeting at an acute angle (Fig. 300, *A*).

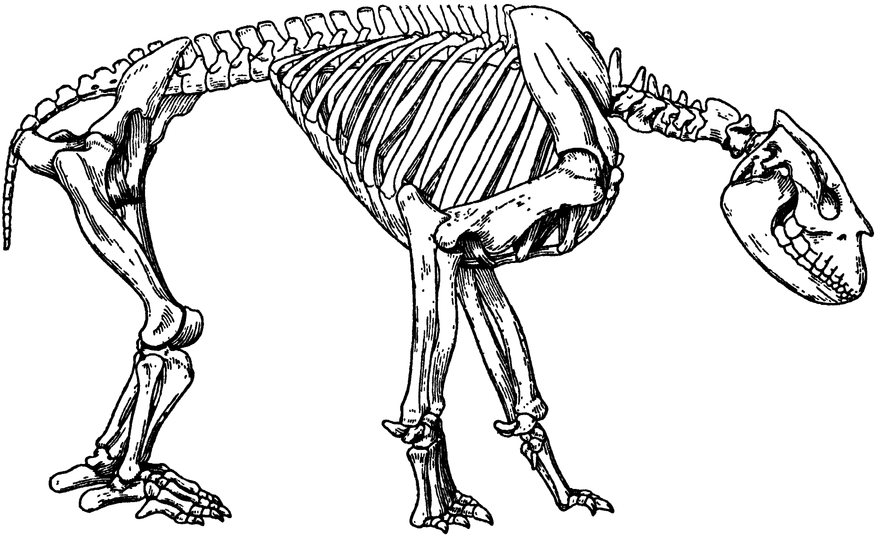


FIG. 297.—*Homalodotherium*, a Miocene entylonychian notoungulate, about 6 feet in length. (From Scott.)

Toxodon (Fig. 302) of the Pliocene and Pleistocene is the largest and one of the latest members of the group and is built like a short-legged rhinoceros. The dorsal position of the nasal opening suggests the presence of a large snout; the general appearance may have been that of a gigantic guinea pig. A diastema, absent in earlier types, had developed in the dentition. *Toxodon* appears to have been the commonest large ungulate of the South American Pleistocene. The Miocene *Nesodon* (Figs. 298, *C;* 299, *B, D;* 300, *A*) was a smaller and more slimly built toxodont the size of a tapir. The dentition was comparatively primitive, for the tooth row was a closed one, although the intermediate teeth (canines and anterior premolars) were small, and the molars finally became rooted late in life. *Adinotherium* was another Miocene form of still smaller size, with a small horn on the frontal bones. Ancestral toxodonts, such as *Proadinotherium* (Fig. 300, *G*, *H*), are present in the Oligocene and others, small and primitive in character, in the Eocene and even the Paleocene (Fig. 300, *E*, *F*).

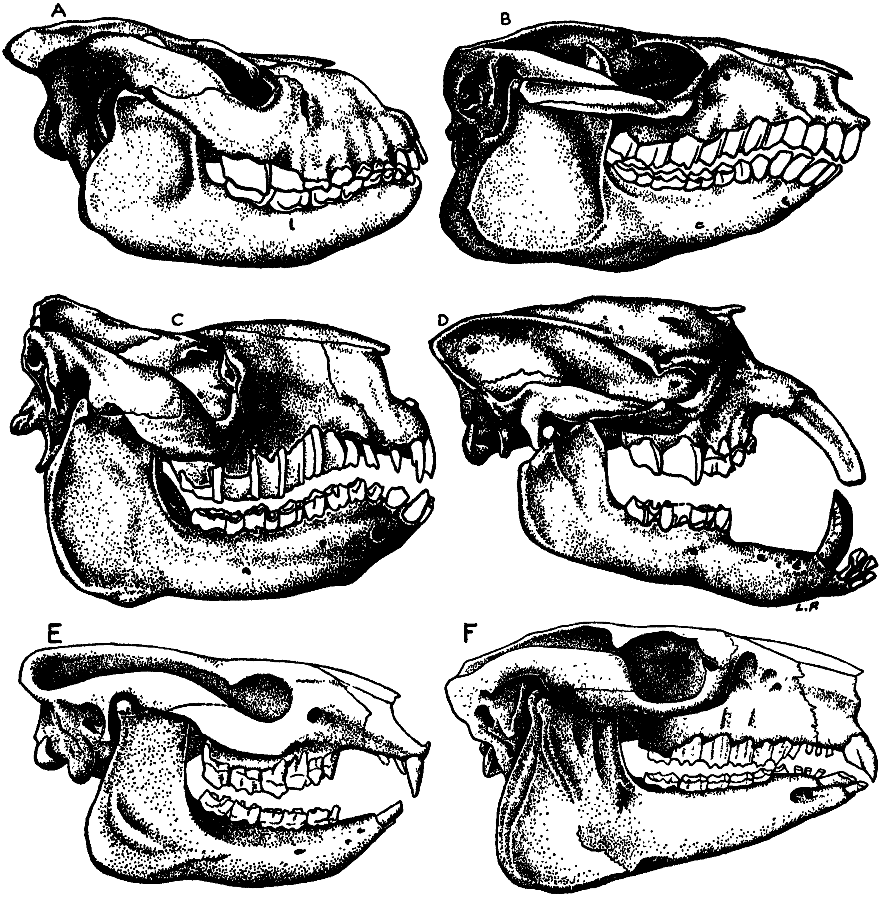


Fig. 298.—Skulls of South American ungulates. *A*, *Homalodotherium* (Miocene), an entylonychian, skull length about 15 inches; *B*, *Protypotherium* (Miocene), a typothere, skull length about 4 inches; *C*, *Nesodon* (Miocene), a toxodont, skull length about 16 inches; *D*, *Astrapotherium* (Miocene), skull length about 27 inches; *E*, *Notostylops*, a primitive Eocene notoungulate (Notioprogonia), skull length about 6 inches; *F*, *Hegetotherium* (Miocene), skull length about 4½ inches. (*A*, *C*, *D* after Scott; *B*, *F* after Sinclair; *E* after Simpson.)

The Oligocene *Leontinia* represents a family rather doubtfully allied to the toxodonts; the facial region was very short, and a high position of the nostril opening suggests the presence of an expanded muzzle or proboscis of some sort.

Notohippus and its Eocene and Oligocene relatives are a poorly known, early side branch of the toxodonts. The complex teeth had some superficial resemblances to those of horses, and it was once claimed that they were members of the Equidae; they were, however, true notoungulates.

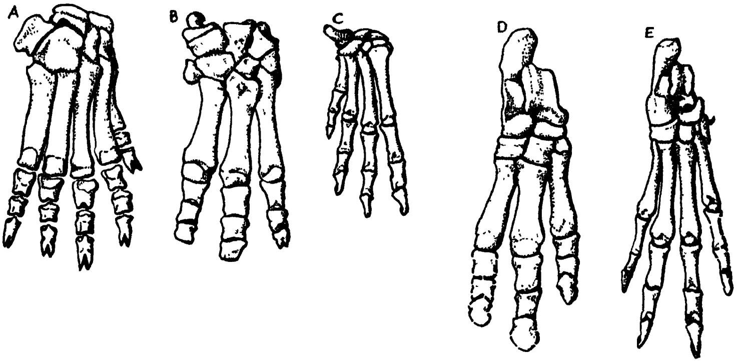


FIG. 299.—Feet of notoungulates. *A*, Manus of *Homalodotherium*, a Miocene entylonychian; *B*, manus of *Nesodon*, a Miocene toxodont; *C*, manus of *Protypotherium*, a Miocene typothere; *D*, pes of *Nesodon; E*, pes of *Protypotherium*. (*A*, *B*, *D* after Scott; *C*, *E* after Sinclair.)

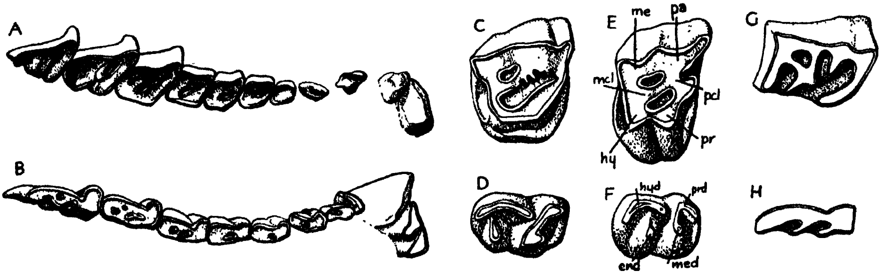


FIG. 300—Teeth of notoungulates. *A*, Upper right, and *B*, lower left, tooth rows of the Miocene toxodont *Nesodon* (×½); *C*, upper right, and *D*, lower left, molars of *Pleurostylodon*, a primitive Eocene entylonychian (×1); *E*, *F*, same of *Oldfieldthomasia*, a primitive Eocene toxodont (×3); *G*, *H*, same of *Proadinotherium*, an Oligocene toxodont (×⅓). Abbreviations, upper molar: *hy*, hypocone; *mcl*, metaconule; *me*, metacone; *pa*, paracone; *pcl*, protoconule; *pr*, protocone. Lower molar: *end*, entoconid; *hyd*, hypoconid; *med*, metaconid; *prd*, protoconid. (*A*, *B* after Scott; *C–F* after Schlosser; *G*, *H* after Loomis.)

Entylonychians.—*Homalodotherium* (Figs. 297; 298, *A; 299, A*) of the Miocene is a last survivor of a group of notoungulates which are present from Paleocene times on and are frequently regarded as constituting a separate suborder, the Entylonychia. The skull, which reached about 2 feet in length, was broad and flat with heavy arches; the nasal opening was farther back on the top of the skull than would primitively have been the case, suggesting a tapir-like snout. The teeth were comparatively primitive for the order, with rather high crowns but closed roots and a very gradual transition in shape from incisors to molars. The molars had a very simple, rather rhinoceros-like pattern, with three main lophs above and two crescents (the front one short) below. As is usually the case in the notoungulates, the pattern tended to become obscure with wear; and in the lower teeth the entoconid, an isolated cusp in primitive notoungulates, is here, as often, merged into the outer crescent.

The limbs of this large end-form were of an odd type. Five toes were present on each foot and terminated not in hoofs but in blunt heavy claws. The hind feet were short and plantigrade, but the front legs were long and powerful. This suggests that *Homalodotherium* was a large root-digger, analogous to the chalicotheres of the Northern Hemisphere.

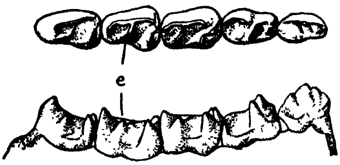


FIG. 301.—Fragment of lower jaw of *Arctostylops*, only known notoungulate from North America, left p_3–m_3, showing the characteristic development of the entoconid (*e*), crown and lateral views. (After Matthew.)

Typotheres.—The suborder Typotheria includes a series of forms which parallel the larger rodents to a considerable degree. *Typotherium* of the Pliocene and Pleistocene was as large as a black bear. Canines and premolars were reduced; the only teeth in the front of the mouth were incisors, one above and two below, the major pair being broad chisels which grow throughout life; the remaining cheek teeth were hypsodont and rootless. The postcranial skeleton was persistently primitive, the foot five-toed, with narrow terminal phalanges. *Protypotherium* (Figs. 298, *B;* 299, *C*, *E;* 303) of the Miocene was a more primitive type, with a complete tooth row and normal incisors. Primitive typotheres are known in the oldest Tertiary deposits of South America.

Another rodent-like group is that of the hegetotheres (Fig. 298, *F*) present from the Eocene to the Pliocene; these forms are often grouped with the typotheres but may merit a separate suborder. Typical Miocene forms were *Pachyrukhos* and *Hegetotherium*. The former was remarkably small for a Miocene notoungulate. It was about the size of a rabbit and further resembled that animal in its stub tail and long hind legs. Its teeth show rodent-like adaptations similar to those seen in *Typotherium*. One cannot but believe that the mode of life of *Pachyrukhos* must have been similar to the rabbits and hares of northern continents. *Hegetotherium* was a larger and more heavily built form, more primitive in the retention (in a reduced stage) of the teeth lost in *Pachyrukhos*.

Notoungulate history.—The history of the notoungulates is indeed a remarkable one. Their presence in the Paleocene of Asia suggests that they must have been one of the very earliest groups to split off from the basic placental stock. Seemingly they constituted a first wave of ungulate development, possibly even older and more primitive than the archaic condylarths and amblypods already considered. Their almost utter absence from the Eocene deposits of the Northern Hemisphere suggests that they were unable to withstand the competition of even those archaic groups, to say nothing of that of the more modernized perissodactyls and artiodactyls.

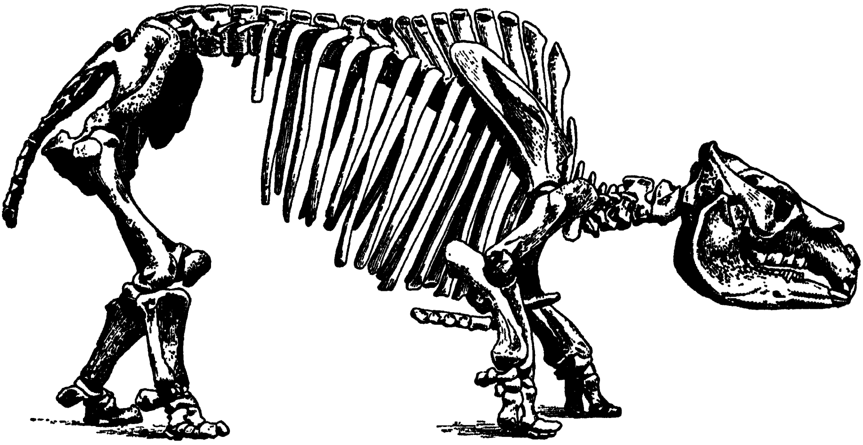


FIG. 302.—*Toxodon*, a large Pleistocene South American notoungulate, about 9 feet in length. (Frcm Lydekker.)

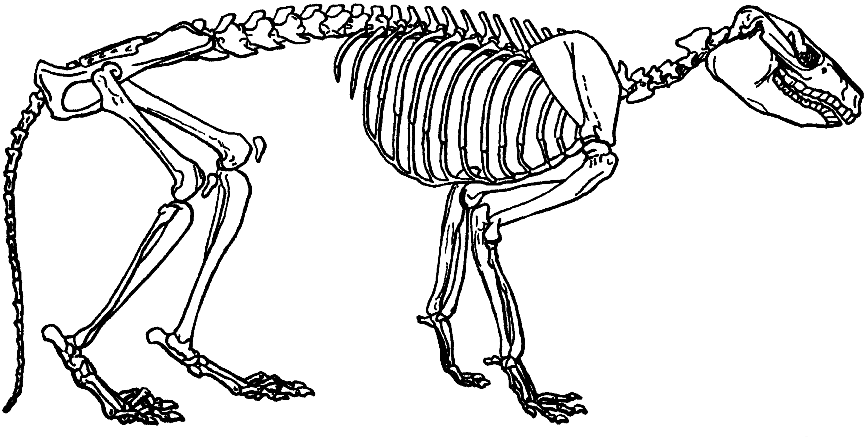


FIG. 303.—***Protypotherium***, a typotherian notoungulate from the Miocene of South America, about 20 inches in length. (After Sinclair.)

But to their early development is due their fortunate inclusion among the few placental groups which had reached South America before the isolation of the continent in earliest Eocene times. For more than half of the Tertiary they flourished there in the comparative absence of herbivore competition or carnivore menace. The peak of their development was reached in the Oligocene and Miocene, when a great many of the notoungulates flourished in Patagonia and presumably in other regions as well. But after this time dissolution set in. In the Pliocene many types of these ungulates disappeared. The irruption into the continent in the Pleistocene of the saber-tooths and other carnivores and of competing ungulates of northern types may have caused havoc among the reduced notoungulate stocks. Today not a single form survives to give us any conception of the appearance, life, or habits of the notoungulates.

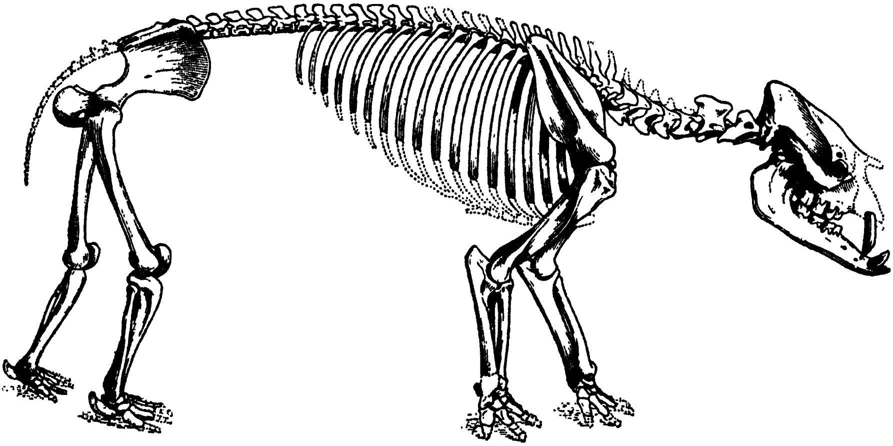


Fig. 304.—*Astrapotherium*, an Oligocene South American ungulate about 9 feet in length. (From Riggs.)

Astrapotheres.—*Astrapotherium* and its relatives of the Oligocene and Miocene of South America are members of a small group once thought to be a component of the notoungulates but now considered a separate order, the Astrapotheria. *Astrapotherium* (Figs. 298, *D*, 304) was a large form, about 9 feet or so in length, remarkably specialized in every regard. The skull looks as if it had been amputated anteriorly, for the upper incisors had been lost and the premaxilla reduced to a nubbin between the huge, curved, and persistently growing canines. The lower incisors were present, however, while the lower canines were also large. Following a marked diastema were vestigial posterior premolars and large molars, the last two of enormous size. The slitlike nasal opening was placed on the upper surface of the skull and was only partially roofed by the short nasals. The presence of large air sinuses in the frontal bones gave the forehead a swollen, domelike appearance.

The situation of the nostrils renders it probable that an elephant-like proboscis was present; the well-developed lower incisors indicate the presence of a tough upper lip to form a cowlike cropping mechanism. What peculiar habits were responsible for the presence of the great canines of this remarkable animal is not at all clear.

Equally puzzling is the postcranial skeleton. The anterior part of the trunk and front legs are rather stoutly built; the hind quarters and legs seem pitifully feeble, and the incompletely known feet defy comparison with those of any other group. All in all, the creature's mode of life is beyond reasonable conjecture, although amphibious habits have been hopefully suggested.

Albertogaudrya of the Eocene was a somewhat more primitive genus without the huge molars of later forms, but the development of the canines was already under way. This astrapothere was tending to gigantism; already of tapir size, *Albertogaudrya* was the largest member of the South American Eocene assemblage, and an Oligocene form was even larger than *Astrapotherium* itself. In the Paleocene and Eocene are found various small forms, such as *Trigonostylops*, which may also belong to the Astrapotheria. Possibly the astrapotheres have come from some primitive notoungulate type; but this is uncertain, and they may have arisen independently from some other archaic ungulate group.

The litopterns.—Still another group peculiar to South America is the order Litopterna. This stock never developed into the multiplicity of types found in the notoungulates but was more orthodoxly ungulate in character. Hoofs were always present, and toe reduction took place on the mesaxonic plan with the development of three-toed types and even a one-toed horselike form. Except for occasional reductions in the incisors, a complete dentition and a closed tooth row were usual features in the order. The cheek teeth were usually low crowned but lophodont, with six-cusped upper molars in which the protocone was large and rather centrally placed. In contrast to the notoungulates the later types built up a postorbital bar.

It is highly probable that the litopterns are condylarth derivatives and in a sense to be regarded as a continuation of that group. We have here classed as condylarths *Didolodus* and its relatives of the Eocene of South America. These types were once regarded as litopterns and exemplify the lack of sharp demarcation between the two orders. Condylarth descent may explain, as parallelism, the resemblances between litopterns and perissodactyls, for the latter group is generally believed to have been derived from condylarth ancestors as well.

Two families were already distinguishable among the earliest litopterns. One, the proterotheres, developed into horselike types. *Diadiaphorus*, of the

Miocene (Figs. 305, 307), was a three-toed form; but in the contemporary genus *Thoatherium* (Figs. 305, 307) we have an ungulate, about the size of *Mesohippus*, which seems more horselike than any true horse, for it was single toed with splints more reduced than those of modern equids. This pseudohorse was, however, comparatively unprogressive in other respects, for the cheek teeth were low crowned and the carpus was poorly adapted for monodactyl running. Parallel to the typotheres was the development of chisel-like incisors (one above and two below); these teeth, however, are more normally developed in other members of the family. This one-toed proterothere became extinct in the Miocene, and only some of the more conservative three-toed types lingered on into Pliocene times.

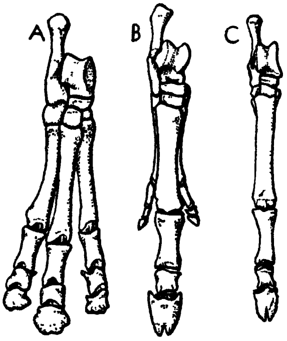


FIG. 305.—The pes of litopterns. *A, Macrauchenia; B, Diadiaphorus; C, Thoatherium.* (After Scott.)

Macrauchenia (Figs. 305, 307) of the Pliocene and Pleistocene was the last surviving member of the order and the most highly developed of a second group of litopterns. The limbs and neck were elongated, and three functional toes persisted. The skull was peculiarly constructed. There was a very long snout which accommodated a well-developed battery of cheek teeth, high crowned, in contrast to other litopterns. The nasal opening was very far

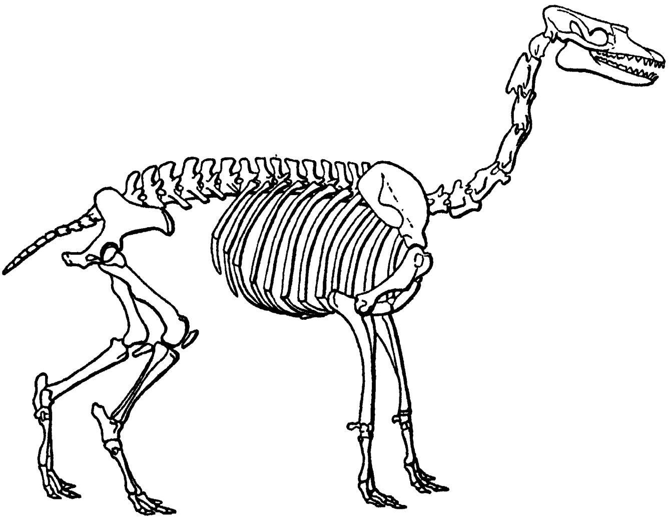


FIG. 306.—The skeleton of *Theosodon*, a Miocene litoptern; length of original about 6 feet. (After Scott.)

back on the top of the skull, much as in some sauropod dinosaurs; and the nasals were vestigial. Some writers have suggested that a proboscis was present, but an alternative explanation is that *Macrauchenia* was a swamp dweller with nostrils dorsally situated for breathing in the water. This form was about the size of a camel and with camel-like proportions. Older and smaller members of this series, such as *Theosodon* (Fig. 306) of the Miocene, were more slenderly built and had lower-crowned teeth and rather longer nasal bones.

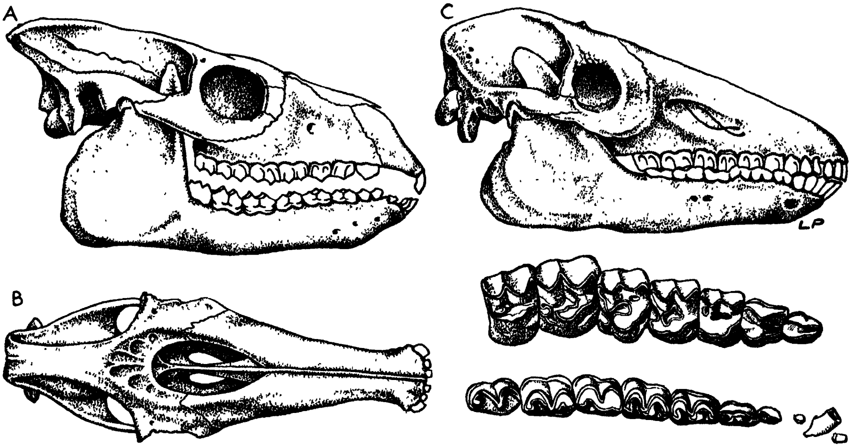


FIG. 307.—Litopterns. *A*, *Thoatherium*, skull length about 7 inches; *B*, *C*, *Macrauchenia*, dorsal and lateral views, skull length about 18 inches. *Lower right*, right upper and left lower teeth of *Diadiaphorus* (×1 approx.). (*A* after Scott; *B*, *C* after Burmeister; teeth after Ameghino.)

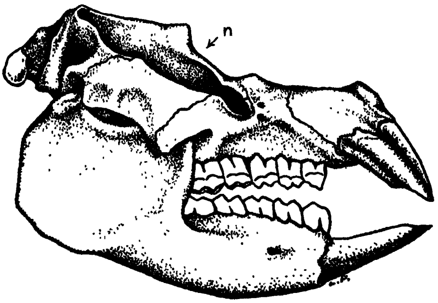


FIG. 308.—The skull of *Pyrotherium*, a South American ungulate paralleling the proboscideans. There is a tusklike development of the incisors, and the nostrils (*n*) are situated above the orbits, suggesting development of a proboscis. Skull length about 2 feet. (After Loomis and Gaudry.)

Pyrotheres.—*Pyrotherium* (Fig. 308), of the Oligocene of Patagonia, is a member of a small, short-lived, and isolated group, the order Pyrotheria, which completes the roster of the South American ungulates. This beast not only had grown at that early time in the Tertiary to the size of an elephant but anatomically had paralleled the proboscideans to a very remarkable degree. The dorsal nasal openings indicate the presence of a proboscis; the facial region was turned upward (rather than downward) on the cranial axis. Above the broad zygomatic arches lay small orbits, behind which no postorbital bar had developed. A heavy transverse crest lay along the top of the occiput for the attachment of strong neck muscles necessary to support the heavy head.

The dentition was strikingly like that of the early proboscideans. Chisel-like tusks were developing out of the incisors, of which but two were retained above (the lateral one large) and one below. Behind a long diastema lay the cheek teeth, six above and five below. As in the earliest proboscideans, these low-crowned teeth were each composed of two cross-crests.

The many similarities in body, skull, and dentition all suggest that *Pyrotherium* was really related to the proboscideans, then developing to the east in Africa. But these resemblances are probably merely a case of exceedingly close parallelism, for the group apparently had arisen in South America. Smaller and more primitive types have been discovered in Eocene rocks of that continent. The dentition of these earlier forms shows, as might have been expected, that the cross-lophed teeth of *Pyrotherium* had been derived (as in elephants) from a bunodont type. But beyond this fact we have no clue as to the origins of the pyrotheres, although obviously they come from some early ungulate stock.

With the pyrotheres we conclude our survey of the native ungulates of South America. These forms owed their successful Tertiary career to their comparative freedom from competing ungulate types and from carnivores, for the advent of these latter forms is unmistakably associated with the disappearance of notoungulates and litopterns. A curious fact, however, is that, despite the disappearance of the native types, few northern ungulates have installed themselves in their places. Mastodons, mammoths, and horses all reached South America but failed to survive. Only the llama group, the peccary, the tapir, and a few deer still exist there. South America is a continent almost devoid of ungulates.

CHAPTER 21

SUBUNGULATES

OFTEN grouped as subungulates are several types of animals which at first sight appear to be unrelated. These include: (1) the hyraces or conies, small Old World hoofed mammals, rodent-like in appearance and habits; (2) *Arsinoitherium,* a huge horned fossil mammal from Egypt; (3) the proboscideans—the elephants and their extinct relatives; (4) the sirenians, or sea cows. It appears incongruous to place together a seeming jumble of land and sea forms, large and small types, but early representatives of these varied groups show fundamental similarities which strongly suggest a common origin; and the fact that the earliest fossil forms are found in Africa suggests that that continent was their common ancestral home.

Because of the great diversity in adaptations which these forms have undergone, it is difficult to find many distinguishing features which hold true of all subungulates. There is usually a greatly enlarged pair of incisors in either jaw, while other front teeth are often reduced; the grinding teeth tend to develop cross-lophs, the premolars become molarized. There is never a clavicle. Usually the land types retain most or all of the digits, with a mesaxonic symmetry, while the primitive claws have developed into structures more like nails than hoofs.

By many these groups are included in an order (or superorder) Subungulata. We shall treat of them as a number of distinct orders, recognizing, however, their close relationship.

Conies.—Most primitive of subungulates in many respects are the Hyracoidea, represented today in Africa and Syria by *Hyrax* [*Procavia*] and related small forms, the conies of the Scriptures. They resemble the rabbits not only in size, general appearance, and habits but also in many adaptive skeletal features. All are herbivores; some are dwellers in rocky country, while others are somewhat arboreal. The tail is short, the legs but moderately long. The gait is plantigrade, with the toes (four in front and three behind) bound together with a pad beneath. There is a centrale in the carpus, unusual in living ungulates.

The skull is of a rather normal construction. Alone among subungulates the living hyraces have a complete postorbital bar. The lower jaw is very deep posteriorly. In living forms there is a considerable amount of reduction in the permanent teeth. In most there is a single, large, rootless upper incisor which meets two enlarged lower ones in rather rodent-like fashion. Behind this the lateral incisors and canines have been lost, leaving a diastema in front of the cheek teeth. The molars tend to be high crowned and rather resemble those of the earlier rhinoceroses in pattern, the upper ones having an ectoloph and two cross-lophs, and the lower teeth a double V. The posterior premolars are molarized; the anterior ones, simpler.

Although none too common today, the hyracoids appear to have played an important role in Africa in earlier times, for the group is represented by a considerable variety of forms, such as *Saghatherium* (Fig. 309, *A*, *E*) and *Megalohyrax* (Fig. 309) in the Lower Oligocene beds of Egypt. These animals were already definitely hyracoid in structure and had even diverged considerably along various adaptive lines. They ranged in size from modest proportions to those of a lion; the teeth varied from brachyodont to high-crowned types, from bunodont to selenodont in pattern. However, they were all more primitive than the living forms, for the postorbital bar was incomplete, the brain small, and the dentition complete (although the teeth later lost were already reduced in size). The later Tertiary history of Africa is poorly known, but conies have been reported from later deposits there and one even from Greece. The fossil types, as well as the living forms, are found

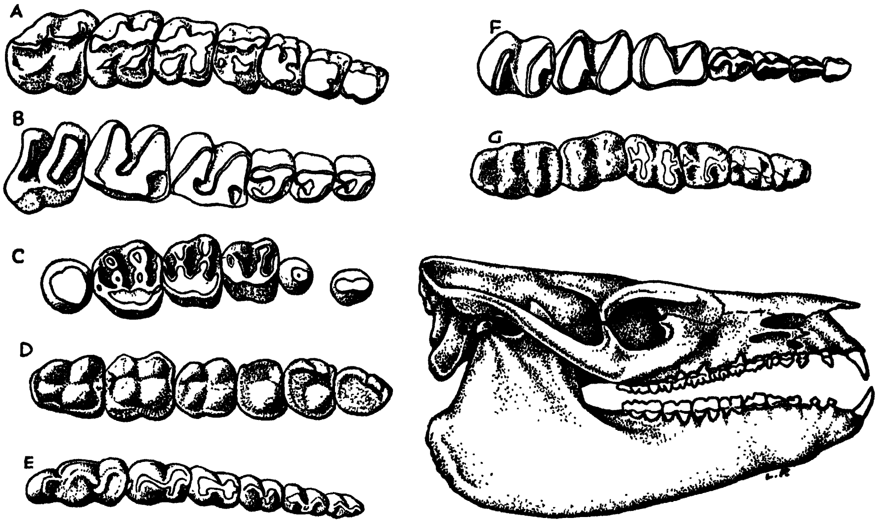


FIG. 309.—Subungulates. *A–D*, Right upper cheek teeth; *E–G*, left lower cheek teeth. *A*, *E*, *Saghatherium*, a hyracoid, $\times\frac{5}{8}$; *B*, *F*, *Arsinoitherium*, $\times\frac{1}{6}$ approx.; *C*, *Miosiren*, a Pliocene sirenian; *D*, *G*, *Moeritherium*, a primitive proboscidean, $\times\frac{1}{3}$ approx. *Lower right*, skull of *Megalohyrax*, a Lower Oligocene hyracoid from Egypt, length about 12 inches. (*A*, *B*, *D–G* after Andrews; *C* after Abel; skull after Gregory and Schlosser.)

exclusively around the eastern Mediterranean and in Africa; the group thus appears to have been characteristically African in origin and development.

Arsinoitherium.—A separate order, the Embrithopoda, is necessary for the reception of *Arsinoitherium* (Figs. 309, *B*, *F;* 310), a peculiar form from the Lower Oligocene of Egypt. This great beast was of rhinoceros size. The limbs were graviportal in structure with long and massive humerus and femur, short lower segments, and a broad, spreading, five-toed foot. The most striking feature of the animal was the presence of a huge pair of horns on the nasal bones, together with small ones on the frontals. The two great horns were fused at their bases, while, much as in some rhinoceroses, an ossification of the partition between the nostrils below aided in their support. The structure of the front part of the skull suggests that there were movable cropping lips, but the tooth row was complete, and there was not the enlargement of incisors seen in other subungulates. The molars were hypsodont (an unusual feature at that early Tertiary date), the upper ones having heavy protoloph and metaloph, while the lower ones had cross-crests showing distinct traces of derivation from the double-V pattern.

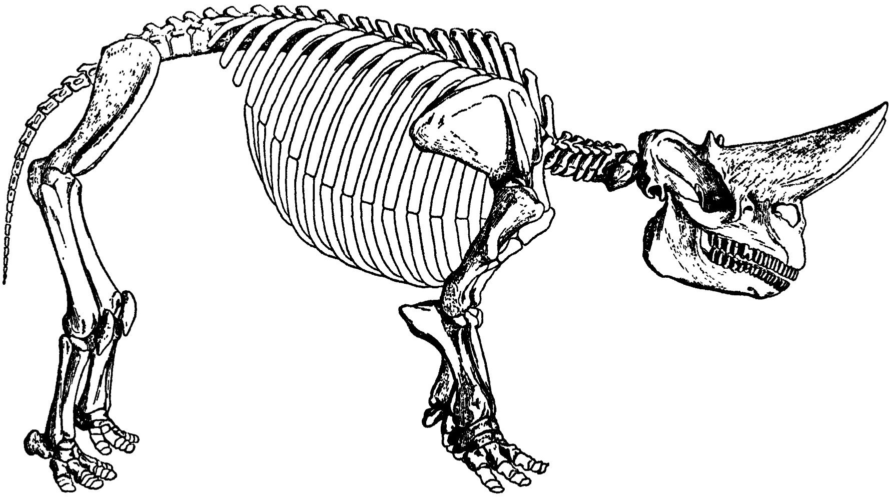


FIG. 310.—*Arsinoitherium,* a large horned subungulate from the Lower Oligocene of Egypt, about 11 feet in length. (From Andrews.)

This curious creature is quite isolated; we know nothing of its ancestors or of any possible descendants. Many points, especially the molar pattern, suggest a common origin with the hyracoids; but the relationship must be a distant one, for the development of the peculiar features of this form must have taken considerable time.

Proboscideans.—One of the most spectacular stories in mammalian evolution is that of the order Proboscidea—the mastodons, elephants, and related types. Like the two preceding groups, they were of African origin but, in contrast with other subungulates, succeeded in invading the other continents and by middle and later Cenozoic times were widespread in Eurasia and North America and even reached South America. Today, however, only two forms survive. We may perhaps best treat this interesting group by describing the highly specialized structures found in the later elephants before taking up the earlier stages in their development.

The elephants and the related Pleistocene mammoths include the largest of late Cenozoic and living land mammals and, as such, have typical graviportal adaptations: an expanded ilium, columnar legs, a long humerus and femur, short lower limb segments retaining a well-developed ulna and fibula, and broad five-toed feet (cf. Fig. 314) with nail-like structures on the outer side of the digits and a pad beneath. The skull (Fig. 311, *D*) is of huge size and roughly rounded shape, with a swollen top which is highly pneumatic. The brain, although reaching 11 pounds in weight in the Indian elephant, is, of course, small compared with the size of the skull. The comparatively small eyes have no bar behind them. The bony nasal orifice lies high up on the front of the skull between the eyes; from it projects the long, flexible trunk. Below this opening the premaxillae descend vertically, bearing the roots of the huge tusks. These are enormously enlarged second incisors. On emergence from the skull the tusks curve forward, upward, and outward. On the short palate the posterior development of the maxillae (in which the teeth develop) is notable. The lower jaw is correspondingly short; in front is a projecting chin superficially like that of man but developed in quite another fashion.

The dentition is remarkable. There are no anterior teeth other than the large upper tusks. In the cheek region the elephants have met the requirement of a large grinding surface in unique fashion. Six teeth develop in each jaw half; these consist of three milk premolars and the three molars (the permanent premolars never make their appearance). Each tooth (Fig. 312, *D*) is elongate and exceedingly hypsodont and is formed of a large number of high, thin, crosswise ridges. The spaces between these "leaves" is filled by cement, so that with wear all three elements of the tooth are exposed in a regular pattern—dentine in the center of the ridges, an enamel band about this, and cement forming the outer portions. The number of ridges increases considerably from earlier to later teeth, the milk premolars being much simpler in structure.

Instead of having all the teeth in place at once, as is usually the case in mammals, the elephants normally have exposed at any given time only four teeth in all, one in each half of each jaw. As these four teeth are worn down,

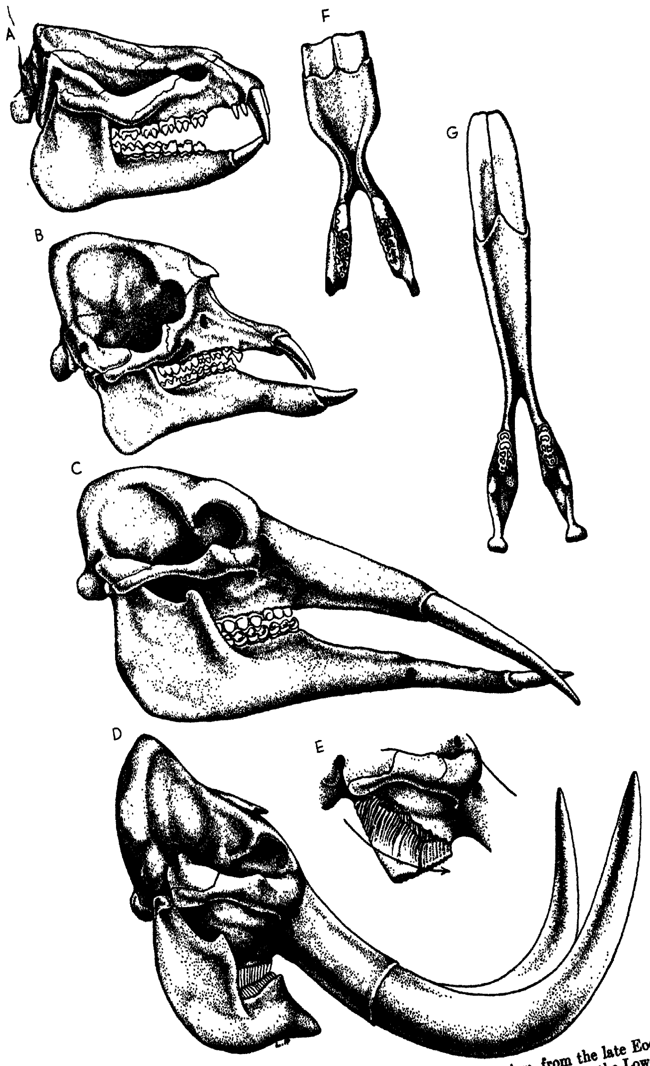


FIG. 311.—The skull and jaws of proboscideans. *A*, *Moeritherium*, from the late Eocene and early Oligocene of Egypt, ×$\frac{1}{8}$; *B*, *Phiomia wintoni*, a primitive bunomastodont from the Lower Oligocene of Egypt, ×$\frac{1}{14}$; *C*, *Gomphotherium* [*Trilophodon*] *angustidens*, from the Miocene of Europe, ×$\frac{1}{30}$; *D*, *Mammuthus primigenius*, the woolly mammoth, ×$\frac{1}{50}$; *E*, diagram of cheek region of the last, with the bone over the molars removed to show direction of tooth replacement; *F*, dorsal view of lower jaw of the late Tertiary mastodon *Platybelodon*, ×$\frac{1}{35}$; *G*, the lower jaws of *Amebelodon*, from the Pliocene of North America. ×$\frac{1}{45}$. (*A*, *B* after Andrews; *C*, *D*, *E* composite; *F* after Osborn; *G* after Barbour.)

they are pushed forward and the next group of teeth, which meantime has been forming in the maxilla or dentary, takes their place (Fig. 311, *E*). This process is repeated until all members of a series are utilized.

Parenthetically, it may be noted that, while teeth are the most common remains of fossil elephants, their interpretation presents difficulties. The appearance of the ridges varies with the degree of wear. The number of plates not only differs from form to form but even more widely from tooth to tooth of the same individual; the premolars are relatively simple, the last molar the most complex.

✓**Moeritherium.**—Very different from the living elephants, but already definitely proboscidean in tendencies, was *Moeritherium* (Figs. 309, *D*, *G;* 311, *A*) of the Upper Eocene and early Oligocene of Egypt, the earliest member of the order. Although much smaller than later proboscideans, it had already reached the size of a tapir. The skull was still fairly long, with the eyes far forward. The nasal opening was somewhat to the top; but the developing trunk was probably little more than a flexible, tapir-like snout.

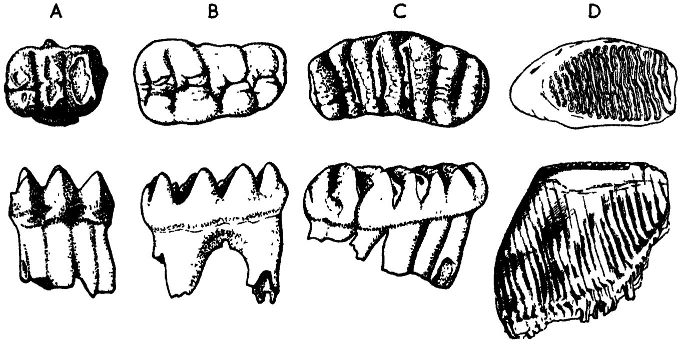


FIG. 312.—Crown views (*above*) and lateral views (*below*) of molar teeth of *A*, American *Mastodon; B*, *Tetralophodon longirostris; C*, *Stegodon; D*, *Mammuthus primigenius*. (*A*, ⅓ natural size; *B* and *C* about ⅙; *D*, about 1/10). (*A* after Hay; *B* after Vacek; *C* after Matsumoto; *D* after Osborn.)

The dentition already shows the beginnings of the proboscidean specializations. The formation of tusks had begun, for the second incisors were much enlarged, the upper one pointing down, the lower one projecting forward to meet it. A diastema was in process of development, and in connection with this the first premolars, the lower canine, and the lateral lower incisor had been lost. The molars were low crowned with two cross-lophs. The limbs were comparatively primitive but already somewhat heavy in build. We have in *Moeritherium* the beginnings of the specializations which led to the later mastodons and elephants. The skull shows many interesting points of resemblance to that of the conies and sirenians; but those groups were already in existence at that time, and their common ancestor must be looked for far back in the Eocene of Africa.

There is considerable evidence that a number of types branched off early from the primitive proboscidean stock. For example, *Barytherium*, a contemporary of the last form, known only from a jaw and a few other fragments, possessed similar bilophodont molars and an enlarged lower incisor. But the jaw was peculiar in other respects, and it is possible that this genus was but distantly related to the proboscideans.

Dinotherium.—Certainly a proboscidean, but obviously far off the main evolutionary path of the group as a whole, was *Dinotherium* (Fig. 313), a large form found fairly commonly in the late Miocene and early Pliocene of Eurasia. The general build was elephantine; and, although the earlier forms were of modest size, later types exceeded most of the true elephants in bulk. The cheek teeth (with but two premolars) were quite primitive, low crowned, and with but two cross-ridges in the back two molars (the first had three). The nostrils were high up on the face, suggesting a long proboscis. While the premaxilla extended well forward, there was, in contrast with all other proboscideans, no trace of an upper tusk. The lower tusk was, however, well developed and curved sharply downward and even backward. What purpose this curious structure could have served is a matter for speculation. *Dinotherium* disappeared from Eurasia during the Pliocene but, like many other primitive forms, survived much later in the tropics and was present in the Pleistocene in Africa.

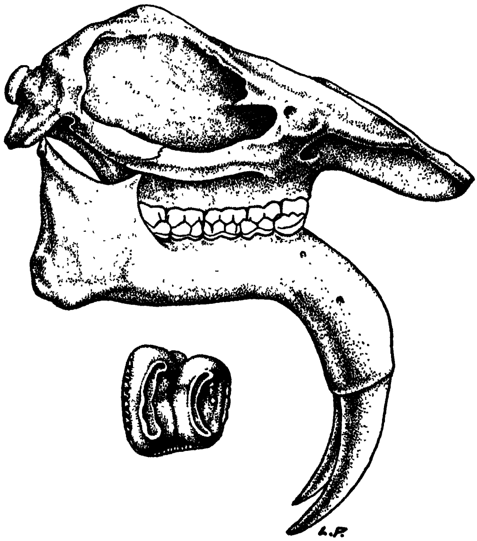


FIG. 313.—Skull of *Dinotherium*, a Miocene proboscidean, length about 47 inches. Molar tooth, ×⅕ approx. (After Gaudry and Andrews.)

Mastodons.—Leaving these divergent forms, we may now return to the consideration of the evolutionary main line represented by the mastodons. These proboscideans, although now extinct, were very numerous and diversified throughout the greater part of the Tertiary. The mastodons may generally be distinguished from elephants by the fact that the teeth were low crowned with few ridges and many or all of the cheek teeth were usually in place simultaneously. Almost always there was a lower, as well as an upper, pair of tusks.

In Egypt, again, appeared the earliest and most primitive of known mastodons, *Palaeomastodon* (Fig. 314, *A*) and *Phiomia* (Figs. 311, *B;* 314, *B*). These Lower Oligocene forms were of larger size than *Moeritherium;* the largest had already reached the proportions of a modern elephant, although the average was much smaller. Structurally, too, they had progressed considerably beyond *Moeritherium.* The braincase was much shorter and higher; the nostrils were placed far up and back on the skull; and the snout must have been long. Of the anterior teeth there remained but a single pair of incisors. These were already well-developed tusks. The upper tusk was borne on the elongated premaxilla and curved downward and outward. The short lower tusks formed a somewhat scoop-shaped affair at the end of the elongated jaw. Premolars (three above, but only two below) and molars were lophodont, low crowned, and all in place simultaneously.

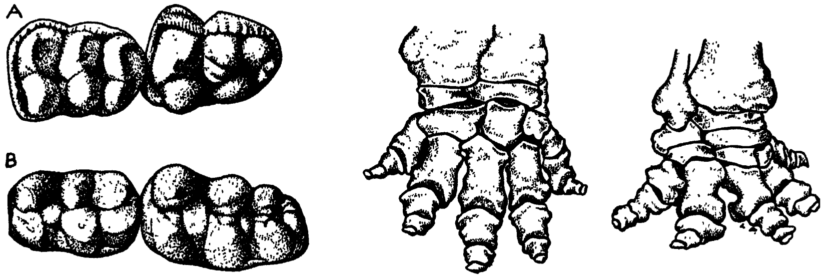


FIG. 314.—*A*, Right M^2–M^3 of *Palaeomastodon beadnelli; B*, left M_2–M_3 of *Phiomia wintoni;* $\times\frac{3}{8}$ approx. (After Andrews.) *At right*, front and hind feet of the American *Mastodon.* (After Warren.)

In *Phiomia* the molars had advanced over those of *Moeritherium* in that three cross-crests were usually present instead of two; and accessory cusps (in addition to the two which normally formed a crest) had begun to make their appearance, tending to make a somewhat bunodont and piglike tooth.

From *Phiomia* appear to have descended most of the later mastodons, characterized by teeth in which a multiplicity of accessory cusps tended to make their appearance. These forms with suid teeth, which may be grouped as the Gomphotheriidae, successfully invaded the northern continents and were present throughout Eurasia and in North America before the end of the Miocene. In these areas they were present in great and bewildering variety during the late Tertiary; only a few persisted into the Pleistocene.

Gomphotherium [*Trilophodon, Tetrabelodon*] was the characteristic Miocene genus (Fig. 311, *C*); the lower jaw was enormously long, bearing short, broad tusks at the end, while the premaxilla was also elongated for the fairly long and slightly decurved upper tusks. The nostrils were high on the skull, but the free portion of the trunk (which presumably began at the end of the premaxilla) must have been comparatively short. Six cheek teeth were present above and five below, all in the jaw at one time, with permanent premolars still replacing the milk premolars. The pattern was becoming more piglike, with an increasing number of irregular cusps; and the number of ridges was increased slightly over *Phiomia*, for, although three were typical, four or five cross-crests were present in the last molar.

Members of the bunomastodont group persisted in the Old World until fairly late in the Pliocene and are even found in the early Pleistocene in Africa. During this time, however, remarkable changes took place which were in many ways parallel to those which must have occurred in the ancestry of the true elephants. *Tetralophodon* was the characteristic Pliocene type. The lower jaw had become greatly shortened, leaving only a very small lower tusk in the end of a chinlike projection of the dentary; the premaxilla, too, had shortened, while from it projected long, straight, upper tusks. With this shortening of the face the fleshy nose above was presumably freed to become a long proboscis such as that found in the modern elephant. The teeth had become somewhat high crowned and had gained some cement. Further elephant-like changes are seen in the loss of replacing teeth for the milk premolars and in the tendency for only a part of the dentition to come into play at once. There was, however, only a gain of a molar crest or so (Fig. 312, *B*), four typically and five in the last molars; and the piglike multiplicity of cusps in the cheek teeth shows that we are dealing with a line that was not ancestral but parallel to that of the true elephants. *Stegomastodon*, a genus which persisted into the early Pleistocene in North America (as did a related form in Asia) and even invaded South America, was still further advanced in jaw abbreviation and increase in cusps to a maximum of seven or eight cross-crests.

The two genera already discussed appear to form the "main line" of evolution of this mastodon family; there were numerous side branches. *Cuvieronius*, representing another set of late Pliocene and Pleistocene survivors in the two Americas, had progressed in the loss of lower tusks and had developed peculiar, spirally twisted upper ones but had retained relatively primitive molars. *Rhynchotherium*, found from Africa to North America in the late Tertiary, retained a long-tusked lower jaw which was curved downward somewhat in the fashion of *Dinotherium*. In *Platybelodon* (Fig. 311, *F*) of Asia and North America and *Amebelodon* (Fig. 311, *G*) of the latter continent, the long, decurved lower jaws bore broad, flat, lower tusks which formed an enormous shovel-like structure. In *Gnathobelodon* of the American Pliocene the lower tusks were absent, but an equally effective shovel was formed by the expanded rostrum of the lower jaw.

While *Phiomia* had three-lobed teeth which tended toward a complicated pattern, the contemporary *Palaeomastodon* retained rather simple, tapir-like, two-lobed molars. This genus may have given rise to a second, less prominent, but long-lived group of mastodons (family Mastodontidae) in which the teeth had a persistently simple pattern, always with low crowns and simple ridges and without cement. Such forms are found in the Miocene (*Mastodon tapiroides*) and Pliocene (*M. borsoni*) of Eurasia, although more rare than the gomphotheres. This group reached America during the Miocene and had as an end-form *Mastodon* proper (Figs. 312, *A;* 315), which persisted in North America throughout the Pleistocene and (as numerous skeletons from postglacial swamps show) probably lived until not many thousands of years ago. In these forms the skull must have changed in a fashion similar to that of the bunolophodonts, for the American mastodon never had more than a vestige of the lower incisor in the short jaw, the skull was high and short, there were huge upper tusks curving upward and outward, and there were never more than two teeth at a time in each jaw half.

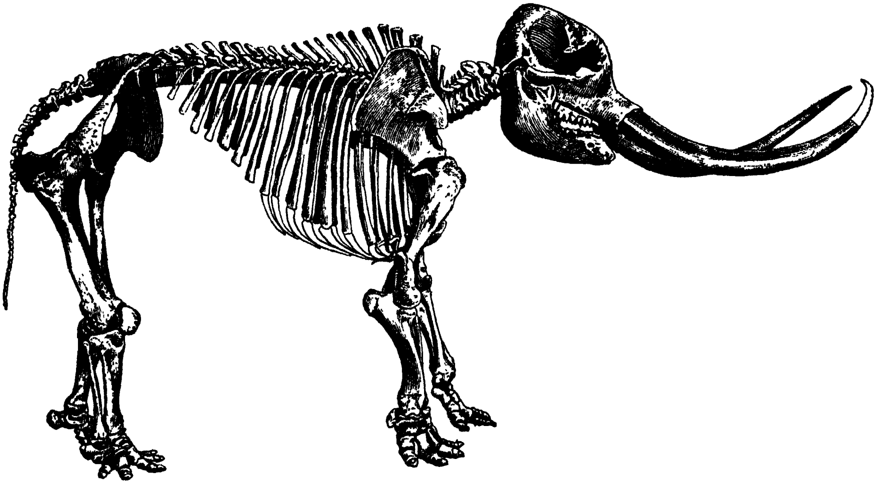


FIG. 315.—The American Pleistocene *Mastodon;* length about 10 feet. (From Hay.)

Elephants.—The family Elephantidae, in which the Recent forms are included, is easily distinguished from a majority of the mastodons through the much higher, shorter head; the huge, curved upper tusks; the short, tuskless lower jaw; and especially by the cheek teeth with their high, cement-covered rows of numerous lamellae and peculiar mode of succession. The elephants are not descendants of any of the well-known mastodon types but appear to have had a long independent history. Seemingly, Asia was the home of the group, and the oldest elephant types are found in the Pliocene Siwalik beds of India. In *Stegodon* of the Pliocene and early Pleistocene of Asia, the skull was somewhat longer than in true elephants; but the teeth (Fig. 312, *C*), while still low crowned, had sometimes as many as fourteen simple ridges with some traces of cement. While there were still traces of the permanent premolars, which have been lost in later elephants, the type of tooth succession was changing, for no more than two at one time were present in a jaw half. Further, the lower-jaw symphysis had been reduced to a chin in which there were only tiny vestiges of the lower tusks, while the upper tusks were long and somewhat spirally curved.

By the end of the Pliocene the first of the typical elephants with short head, tuskless lower jaws, and high-crowned, cement-covered teeth had appeared in southern Asia and Europe; and in the Pleistocene various elephant types usually referred to as "mammoths" were abundant in all the northern continents. The matter of proper usage of generic terms for these forms is in a confused state. At one time all were included in the genus *Elephas*, using that term in a broad sense; recently there has been a tendency to split the elephants into a large number of genera. We shall here group the characteristic Pleistocene and Recent forms in three genera: *Loxodonta*, *Elephas*, *Mammuthus*.

Typical of *Loxodonta* is the living African elephant; the molars are rather narrow and relatively low crowned, with a comparatively small number of ridges, which, with wear, tend to show a rhomboidal pattern. The head is not so short or deep as in other late elephant types; the tusks are long but are little curved. *Loxodonta antiqua*, the straight-tusked "ancient elephant," was an inhabitant of southern Europe and northern Africa in the Pleistocene. Some specimens reached a height of 14 feet at the shoulder; on the other hand, dwarf races of this form, some no larger than a pig, have been found as fossils on Mediterranean islands. Other loxodonts occur in the Pleistocene of Asia.

Elephas, as used here, is typified by the living Indian elephant. In contrast with the loxodonts, the skull is very short and deep, with a rounded vault; the tusks are short and straight and, again contrasting with loxodonts, are directed more downward than forward from their sockets. The molars are broad and high and with numerous closely appressed ridge-plates. Relatives of the living species were present in the Pleistocene of Asia and the East Indies.

Most interesting of fossil elephants is a great array of forms to which the term "mammoth" is usually applied and which are here gathered into the genus *Mammuthus*. In these mammoths the tusks are vertically directed at their bases, as in *Elephas*; however, they are much elongated and curved and may even cross one another, in old males. The skull tends to be even shorter and higher than in the Indian elephant and has a pointed roof. The teeth are constructed much as in *Elephas*, but the number of plates is variable. In some early and primitive Asiatic species even the last molars have but ten or a dozen plates; these teeth in some woolly mammoths have the extreme figures of twenty-seven to thirty ridges. In this genus are included a number of prominent Pleistocene forms. *Mammuthus planifrons* of the early Pleistocene of Asia was a primitive type; *M. meridionalis*, the southern mammoth common in the Mediterranean region, was closely related; *M. imperator*, the imperial mammoth of southern North America, was more advanced in size and dental development. The form characteristic of temperate North America, usually termed the "Columbian mammoth," was not exceptionally large but had highly developed molars. *Mammuthus primigenius* (Figs. 311, *D;* 312, *D*), the woolly mammoth, was a form adapted to cold climates, common throughout the Pleistocene in the northern parts of both Eurasia and North America. It is known not only from skeletal remains but also through the many figures made by paleolithic man on cave walls and through complete cadavers unearthed in the frozen tundras of Siberia.

Sirenians.—A final order, the Sirenia, includes the most aberrant of subungulates. These forms, manatees and dugongs, or sea cows, are not ungulates in any normal sense but are purely aquatic animals, found along the coasts and river mouths of various parts of the world. The skin of living sirenians is nearly naked and tough and leathery. The body has assumed the torpedo-like shape characteristic of many water vertebrates, with no distinct neck and with a laterally expanded tail. Here, as in other groups, the front legs have been transformed into flippers, while there is no surface indication of the vestigial hind limbs and pelvis. A characteristic feature of the skeleton of manatees is that much of the bone has a compact structure—pachyostosis—seen in certain other aquatic vertebrates (the mesosaurs, for example).

The brain (and consequently the cranial cavity) is small. Only in the case of one living form is the postorbital bar developed. The premaxillae form a long, high, and narrow rostrum, usually curved downward, with the paired nostril openings placed above and well to the rear; the nasals are vestigial. The lower jaw is heavy and has a long symphysis in front. The modifications of the front limbs are not so great as in the whales, for there is still considerable freedom of movement at the elbow and wrist and in the fingers. There tends to be fusion of carpal elements, however. The thumb is reduced; but, while the other fingers may have but two joints, the number may increase to four.

Living forms possess a pelvis (Fig. 316) which is only a solid plate or rod without subdivisions and without bony connection with a sacral rib; nothing remains of the hind limb.

Like their terrestrial subungulate relatives and in contrast with other types of aquatic mammals, the sea cows are purely herbivorous. The dentition of living forms is quite specialized and reduced anteriorly. The dugong has merely a pair of upper incisor tusks, while the manatee has no front teeth at all as an adult; in both types horny plates form a substitute cropping organ. The cheek teeth in primitive forms and in the living manatees have two cross-crests, as in primitive proboscideans.

Primitive sirenians.—Remains of sea cows are not uncommon in the Eocene beds of Egypt. While this fact suggests an African origin, their migrations must have begun at an early date, for an early sirenian is also reported from Jamaica. Very primitive sirenians are *Protosiren* (Fig. 316) of Egypt and the Jamaican form, *Prorastomus; Eotheroides* [“*Eotherium*”], commonest of the Egyptian finds, is somewhat more advanced in the direction of the dugongs. The early genera show definite sirenian characteristics, such as the posterior retreat of the nostrils, the presence of two-ridged molars, and the beginning of pachyostosis. They were, however, more primitive in many ways than the modern forms. The snout is but little down-turned, and in *Prorastomus* the tooth row forms practically a straight line. Nasals and lacrimals, vestigial in later sirenians, were unreduced. The entire series of normal placental teeth is present; in specimens of *Prorastomus* and *Protosiren* one of the milk molars is retained in the adult, suggestive of a trend toward the increased number of teeth noted below for the manatees. Even in *Eotheroides* the pelvis was quite well developed (Fig. 316), while the hind legs appear to have been complete and still functioning, although of small size.

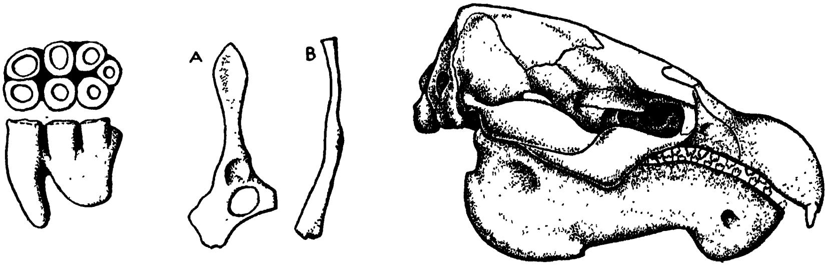


Fig. 316.—*Left*, crown and side views of a molar tooth of the Miocene *Desmostylus*, × ⅓. (After VanderHoof.) *Center*, pelvis of *A*, an early sirenian, *Eotheroides*, and *B*, the modern Dugong. (After Abel.) *Right*, restored skull of the primitive Eocene sirenian *Protosiren*; length of original about 13 inches. (Mainly after Sickenberg.)

Dugongs.—The dugong, the “mermaid” of the Red Sea and Indian Ocean, is the sole survivor of a group very common as fossils throughout the Tertiary. There is a massive beak bent down above the heavy lower jaw. Of the front teeth, which are mainly replaced by a heavy, horny, rubbing pad, there remain only vestiges except for upper incisor tusks in the male. The premolars are degenerate, and the permanent set never develops, while the molars are large and, with a wrinkled surface and many bunodont cusps, superficially resemble those of the pigs or the bunomastodonts.

A tendency in the dugong direction was already apparent in some of the Eocene sirenians, such as *Eosiren*. The beak was already slightly tilted, nearly the full complement of teeth was still present, but the first incisors were somewhat enlarged; the number of cusps in the molars was already tending to increase, and the intermediate teeth were much reduced in size. In later Tertiary deposits, especially in Europe, there have been found a considerable number of forms leading toward the living type. Some, such as *Halitherium* (Fig. 317) of the Oligocene and early Miocene, *Metaxytherium* of the late Miocene, and the Pliocene *Felsinotherium*, are quite well known. In them a lower incisor tusk persisted for some time but finally disappeared along with the smaller remaining front teeth. The beak was bent downward in dugong fashion, the pelvis was reduced, and the hind legs dwindled and vanished.

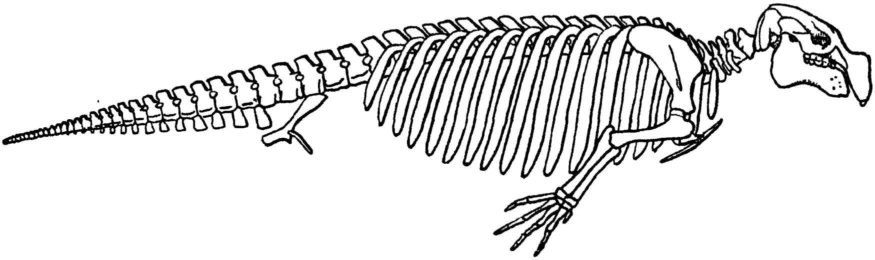


FIG. 317.—*Halitherium*, an Oligocene sirenian, about 9 feet in length. (Simplified from E. von Stromer, *Lehrbuch der Palaeozoologie*, Vol. 2 [Leipzig: B. Teubner].)

Through most of the Tertiary various side lines of this family are known, of which perhaps the strangest was that which ended with Steller's sea cow, *Rytina*, found by the Russians in the Bering Sea and exterminated by them nearly a century ago. Here both the tusks and the entire set of cheek teeth had disappeared, to be replaced by rubbing plates.

Manatees.—A second living group is that of the manatees, *Manatus*, inhabiting the Atlantic shores of Africa and America. A feature unique among mammals is that there are here but six cervical vertebrae. The beak, while long, is not markedly decurved. All the front teeth have disappeared. The bilobed cheek teeth have undergone a curious development. Their number in each jaw ramus has increased to twenty or more, of which five or six may function at one time. The method of replacement is quite peculiar; the teeth form at the back of the jaw, and as they function, push forward until they are worn down and disappear at the forward end of the tooth row. This type of tooth replacement is reminiscent of that of the later mastodons and elephants. Almost nothing is known of the history of the manatees.

Desmostylus.—Found in marine Miocene deposits on both sides of the North Pacific are the teeth and (rarely) the skulls of a peculiar aquatic animal, *Desmostylus* (Fig. 316). The cheek teeth were peculiar in structure, the large posterior ones consisting of a number of cusps (eight above, seven below) developed as closely packed, heavily enameled cylinders; these teeth suggest a mollusk-eating mode of existence, contrasting with that of typical sirenians. As in proboscideans and manatees, the cheek teeth are replaced by means of a horizontal forward movement. The anterior teeth are present, in part, as tusks—an upper pair formed by the canines, two lower pairs formed by incisors and canines.

In a number of respects the skull differs from that of typical sirenians: it is low, and the snout is broad and turned downward but little. The jugals are small. The external nares remain anteriorly placed; and, although the nasals remain well developed, they do not enter the border of the nostrils.

Despite these differences and despite lack of data on the postcranial skeleton, it is generally held that *Desmostylus* is a sirenian, although best placed in a separate suborder. We know nothing of the history of the group except the presence of a somewhat smaller related form in the Oligocene of Pacific North America.

The earliest sirenians, as we have seen, showed very clearly their derivation from land forms; and the fact that so many early remains are from Egypt suggests Africa as the continent of origin. The primitive complete dentition, with large incisors and molars with cross-lophs, is suggestive of that of the early elephants, while many details of skull structure are highly comparable with those of both elephants and conies. The evolutionary tendencies shown in later members of the order are also similar to those of the proboscideans in such respects as the development of a single pair of incisor tusks, the tendency toward a polybunodont type of cheek tooth, and the tooth replacement of the manatee, essentially similar to that of the modern elephant.

All in all, our study of the various groups discussed in this chapter tends to confirm the seemingly odd assumption of the relationship of the diversified subungulate forms. But, although the early Egyptian fossils seem to be approaching the common type from which the subungulates have been derived, conies, proboscideans, and sirenians were already distinct groups at that time. It is only through some future discovery of very early Tertiary deposits in Africa that we may hope to find the common ancestor of the late subungulate orders.

CHAPTER 22

PERISSODACTYLS

AMONG all vertebrates there is, perhaps, no group whose fossil history is better known than that of the order Perissodactyla, the "odd-toed" ungulates. Although represented at the present day by but a few species of tapirs, rhinoceroses, and horses, perissodactyls were numerous throughout the Tertiary and included not only the ancestors of these living groups but also such interesting extinct types as the huge, horned titanotheres and the grotesque, clawed chalicotheres.

Limbs.—As usual with ungulates, the locomotor apparatus has been of importance in the evolutionary history. In most perissodactyls the limbs have tended to become long and slim, with a lengthening of the distal segments as compared with the proximal ones, while the ulna and fibula may be reduced. There is, as usual in ungulates, no clavicle; but in contrast with the artiodactyls (or even-toed ungulates) the femur has a well-developed third trochanter. The carpus is of the alternating type. The upper end of the astragalus has a well-keeled surface for the tibia; but, unlike the artiodactyls, this is not duplicated at the lower end, which is, at the most, rounded (Fig. 286).

The feet (Figs. 319, 328, 329) are of the mesaxonic type, with reduction usually taking place to three toes or even to one in late horse types. In the hind foot the earliest-known forms had already reduced the number to three, with only metatarsal splints representing the first and fifth digits. But the first stage in reduction in the front foot led to a four-toed condition common in the Eocene; for, while no trace of the thumb has been found in even the earliest of perissodactyls (except in a chalicothere), typical early forms had retained all the other toes, although the outer one was somewhat weak. This stage in toe reduction, with four digits in front and three behind, is retained to this day by the tapirs. But beyond the Lower Oligocene other surviving types had no more than three toes on each foot.

Teeth.—Equally characteristic of the group is the tooth development (Figs. 320, 321). The full complement is found in many early forms, but there may be various losses and specializations in the incisors and canines, and a diastema almost always develops, the first premolar being sometimes lost in the process.

The upper molars in the most primitive forms known had already gained a hypocone and (as seen in a very primitive horse [Fig. 241, *B*]) showed six bunodont cusps, the intermediate conules being primitively well developed. Typically, a lophodont condition arises from this (Fig. 243). An ectoloph, often W-shaped through the development of the external row of styles, occurs in most forms. Transverse ridges, protoloph and metaloph, are found in three of the five main groups; but, on the other hand (in titanotheres and chalicotheres), the inner cusps may retain a bunodont condition. In the lower molars a pair of V's usually develops from the original trigonid and talonid and may become a W-shaped structure through union of their adjacent ends or have their main posterior limbs changed into transverse crests. The teeth may remain low crowned, as in the early forms, while in others (especially in the horses) the teeth may become markedly hypsodont.

Complete molarization of most of the premolars is general among later members of the group. In some cases, as in the horses, the process has been carried so far that there is almost complete identity in appearance. These highly developed teeth are in contrast with the small and undeveloped premolars found in artiodactyls.

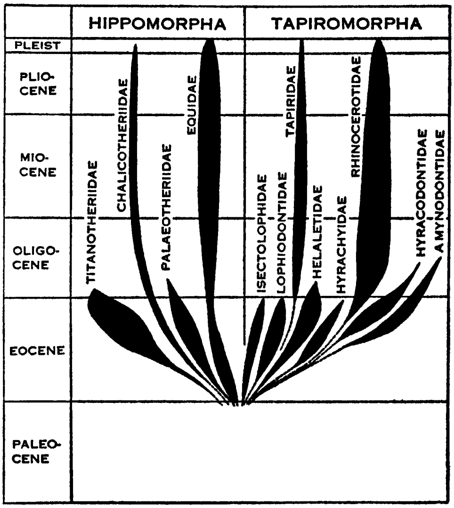


FIG. 318.—The phylogeny of the perissodactyls

The facial part of the skull (Fig. 323) is usually rather long in connection with the development of a long series of grinding teeth. A postorbital bar is developed only in the later horses. The nasals are broad posteriorly and usually extend freely well forward over the nasal opening. Hornlike structures have developed in the titanotheres and many rhinoceroses.

Horses.—The order may be divided into subordinal groups, of which we shall first consider the Hippomorpha, the horses and their relatives, most progressive of all perissodactyls. In the horses there is almost no loss of teeth, the incisors being retained and forming chisel-shaped cropping organs. Cross-lophs slanting back from the ectoloph are developed on the upper cheek teeth; the intermediate conules tend to retain their individuality and thus make in many cases a very complicated pattern. There was an early reduction of toes to three in the front as well as the hind foot, and in later types a progressive reduction toward and to a monodactyl condition.

A discussion of the structure of the modern end-forms constituting the genus *Equus* (horses, asses, zebras) gives a good introduction to horse history. The modern horse has the most highly specialized limb structure of any perissodactyl. In its mechanism it is almost perfectly adapted for rapid forward movement on hard ground and almost incapable of any other type of movement. The humerus and femur are short, powerful, driving segments from which depend the much longer radius and tibia, the main supporting elements of the front and hind feet, respectively. The shaft of the ulna is reduced and fused to the radius; while of the fibula there remains only a splint above and a vestige fused to the tibia below. Only one toe, the third, is well developed (Fig. 319, *D*); this has a much elongated metapodial but short phalanges, the terminal one expanded into a semicircular structure supporting the hoof. Of the side toes, splints of the metapodials remain; nubbins on their ends may represent the lost digits. The carpals are arranged in two semicircular layers between the radius and the metacarpal, with the magnum (the normal support for the third finger) enlarged and the first carpal vestigial. Similarly in the tarsus the ectocuneiform plays a prominent part in carrying the weight from the well-keeled astragalus and the underlying navicular to the toe.

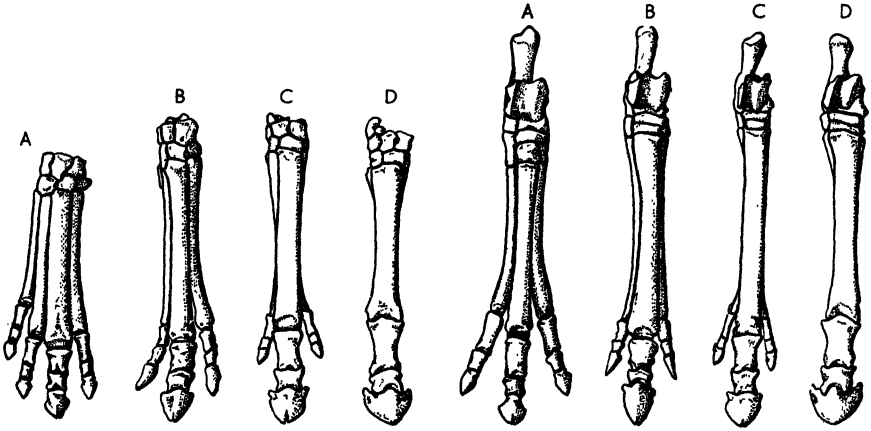


FIG. 319.—Feet of horses. Manus at left, pes at right. *A*, *Eohippus*, a primitive Lower Eocene perissodactyl with four toes in front, three behind; *B*, *Miohippus*, an Oligocene three-toed horse; *C*, *Merychippus*, a late Miocene form with reduced lateral toes; *D*, *Equus*. (*A* after Cope; *B*, *C* after Osborn.)

All the incisors are present in the modern horse; broad and in a closed row, they form an efficient cropping mechanism. Behind them is a long diastema, in which lies the small and variable canine. The first lower premolar is absent, but the small upper one lies at the front end of the grinding battery (Figs. 320, *B*; 321, *B*). This is composed of six teeth in each jaw half, the molars and premolars almost identically constructed. The cheek teeth are very high crowned with a complicated prismatic pattern, the aspect of which changes somewhat with wear as the siliceous food grinds down across enamel and dentine and across the cement which fills the interstices and covers the tooth. The pattern, though complicated, can be identified with the primitive bunodont and lophodont conditions found in early equids (Fig. 322). In the upper molars the ectoloph is represented by two crescents for the paracone and metacone, with projections formed by the parastyle, mesostyle, and

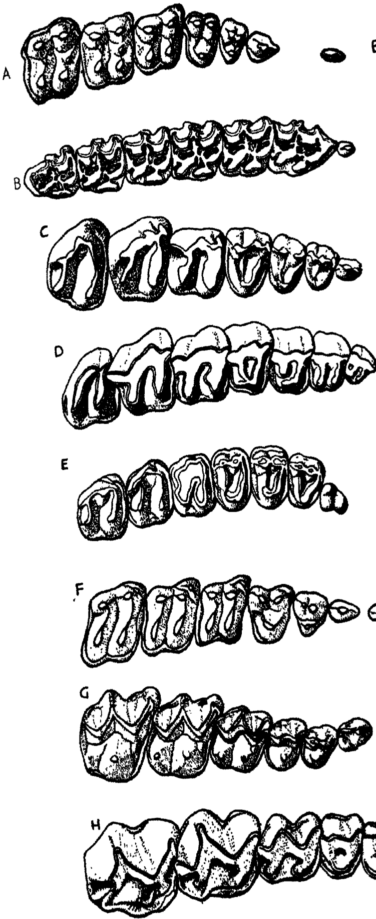


Fig. 320.—(*Left*) Right upper cheek teeth of perissodactyls. *A*, *Eohippus*, ×1 approx.; *B*, *Equus occidentalis* (Pleistocene), ×½ approx.; *C*, *Hyrachyus*, ×3/5 approx.; *D*, *Caenopus*, ×3/5 approx.; *E*, *Protapirus validus*, ×5/9 approx.; *F*, *Homogalax*, an Eocene tapiroid, ×1; *G*, *Palaeosyops*, ×5/12 approx.; *H*, *Moropus*, ×1/3. (*A*, *B*, *F* after Matthew; *C*, *D*, *G* after Osborn; *E* after Hatcher; *H* after Peterson.)

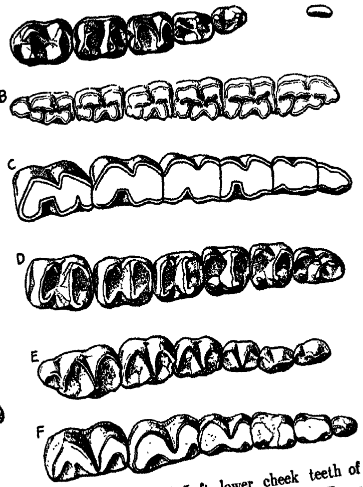


Fig. 321.—(*Above*) Left lower cheek teeth of perissodactyls. *A*, *Eohippus*, ×1 approx.; *B*, *Equus leidyi* (Pleistocene), ×½ approx.; *C*, *Diceratherium*, ×3/7 approx.; *D*, *Protapirus validus* (Oligocene), ×5/9 approx.; *E*, *Limnohyops*, ×5/12 approx.; *F*, *Moropus*, ×1/3. (*A* after Wortman; *B* after Simpson; *C*, *F* after Peterson; *D* after Hatcher; *E* after Osborn.)

metastyle. Anteriorly a crescent swings inward as the protoconule. Internal to this is the nearly isolated protocone; while the posterior end of the protoconule connects with the metaloph, developed internally into a crescentic hypocone. From this last, in turn, a ridge representing the hypostyle runs outward toward the posterior end of the ectoloph. This much-folded pattern, presenting alternating layers of three different substances, forms a highly effective grinding organ. The lower teeth have had a similar history, but the pattern is obviously derivable from a primitive one in which a connecting link between the two V's is afforded by a metastylid adjacent to the metaconid.

The facial part of the skull (Fig. 323, *B*) is elongated in relation to the long set of cheek teeth and the diastema. In the modern horses there is a postorbital bar.

Eocene horses.—The modern horses and their relatives are almost perfectly adapted in both limbs and dentition for a grazing, plains-dwelling life. Far different in structure and probable habits were the earliest horses, found in the Lower Eocene. Best known is the American *Eohippus* (Figs. 319, *A;* 320, *A;* 321, *A;* 322, *A;* 323, *A;* 324); this genus was close to, if not identical with, the contemporaneous *Hyracotherium* of Europe. *Eohippus* was a small form, no larger than a fox terrier. The skull had but a short facial region, the orbits (lacking, of course, a postorbital bar) lying in the middle of its length. All the teeth were present, and there was but a short diastema. The low-crowned molars were already squared up with six cusps present above and four below. There was here just the beginning of a tendency toward loph formation, but the tooth was still essentially bunodont in character. The premolars were still comparatively simple, none of the upper ones having progressed beyond a triangular shape. The limbs were moderately long and slim, with the metapodials rather elongated and with definite hoofs on the end-phalanges. The toes were already reduced in number. In the front foot

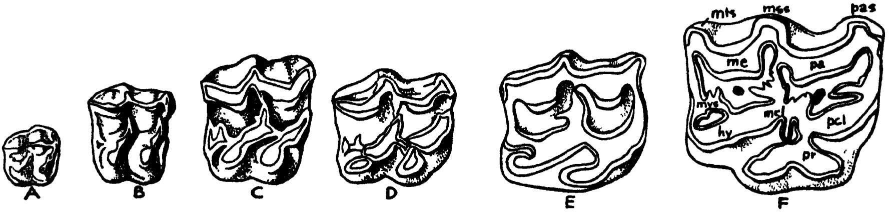


FIG. 322.—Right upper molar teeth of various horse types, all natural size. *A*, *Eohippus* (L. Eocene); *B*, *Mesohippus* (Oligocene); *C*, *Parahippus* (L. Miocene); *D*, *Merychippus* (U. Miocene); *E*, *Pliohippus* (Pliocene); *F*, *Equus complicatus* (Pleistocene). The complicated cusp pattern of the modern horse tooth may be traced back to the comparatively primitive condition in *Eohippus*. Abbreviations: *hy*, *hypocone; hys*, *mys*, hypostyle; *mcl*, metaconule; *me*, metacone; *mes*, *mss*, mesostyle; *mts*, metastyle; *pa*, paracone; *pas*, parastyle; *pcl*, protoconule; *pr*, protocone. (After Matthew.)

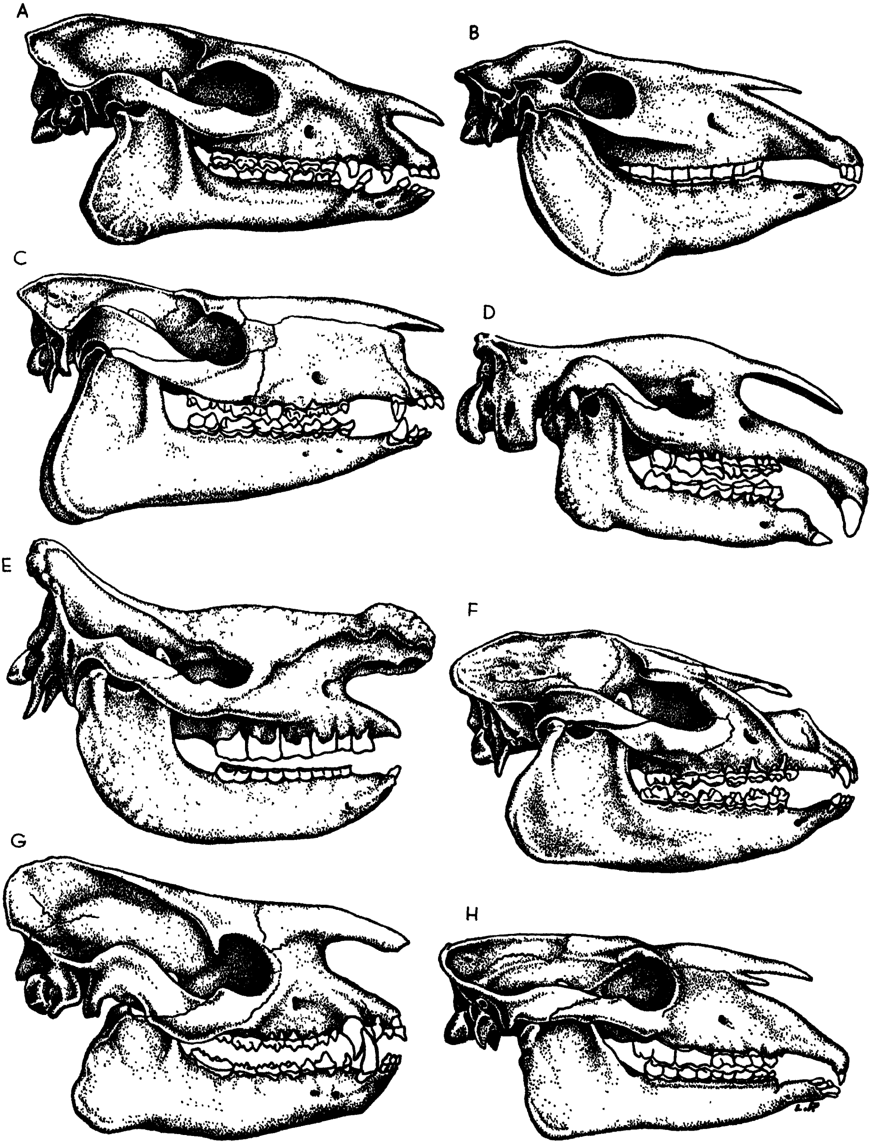


FIG. 323.—Skulls of perissodactyls. *A*, *Eohippus*, skull length about 5½ inches; *B*, *Equus niobrarensis*, a Pleistocene American horse, skull length about 23 inches; *C*, *Hyrachyus*, an Eocene hyracodont, skull length about 11½ inches; *D*, *Baluchitherium*, a giant hornless Oligocene rhinoceros, skull length about 4½ feet; *E*, *Diceros pachygnathus*, a Pliocene horned rhinoceros, skull length about 2 feet; *F*, *Protapirus validus*, an Oligocene American tapir, skull length about 1 foot; *G*, *Limnohyops*, an Eocene hornless titanothere, skull length about 15 inches; *H*, *Moropus*, an American Lower Miocene chalicothere, skull length about 2 feet. (*A* after Cope; *B* after Hay; *C* after Scott; *D*, *G* after Osborn; *E* after Gaudry; *F* after Hatcher; *H* after Peterson.)

all traces of the thumb had disappeared; but the other four toes were all functional, although the outer one was comparatively small. In the hind foot only three toes were present; but there were traces of the missing digits in the form of metatarsal splint bones. This small, forest-dwelling browser is of great interest. Unquestionably, it stands at the base of the horse series. But, even more than that, it exhibits many features to be expected in the ancestors of other perissodactyl families and, without doubt, was very close to the roots of the whole perissodactyl stock.

In the Middle and Upper Eocene of North America we find, in *Orohippus* and *Epihippus*, descendants of this primitive equid in which the structure was essentially the same and in all of which four toes were retained in the front foot. A few advances, however, did take place: the splints disappeared in the hind foot, and the last two premolars took on more of the molar pattern.

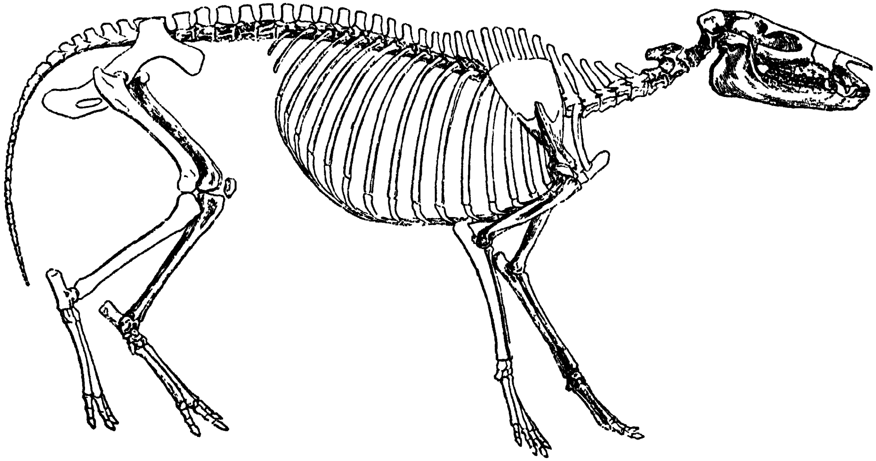


FIG. 324.—*Eohippus*, the "dawn horse" of the Lower Eocene, probably close to the stem of the perissodactyls; length about 18 inches. (After Cope, from Smith Woodward.)

Mesohippus and related types.—The next main stage in horse evolution begins in the Lower Oligocene, again in North America. There, in *Mesohippus* (Figs. 322, *B;* 325), typically the size of a collie, and the somewhat larger *Miohippus* (Fig. 319, *B*) we find the beginning of a series of functionally three-toed horses. In the front foot the outer toe has gone, although a vestige of its metatarsal persisted in many later equids. The metapodials of the three remaining toes were much more elongated than in Eocene types; but while the central toe was somewhat larger, all three undoubtedly reached the ground.

The diastema had continued its development; and, while the cheek teeth were still low crowned, all the premolars except the small first one had become completely converted to the molar pattern. This pattern was now definitely lophodont, with a typical W-shaped ectoloph above but with the cusps constituting the cross-lophs retaining their individuality. At the back edge of the upper molars the hypostyle was beginning to be prominent. In the lower jaw there were two crescents with a distinct double cusp (metaconid and metastylid) at their junction.

The teeth and feet of these typical Oligocene horses suggest that, like their ancestors (and the tapirs today), they were essentially browsing forms, living on soft vegetation in forests and glades where their spreading, three-toed feet would enable them to go over soft ground difficult for the later, single-toed horse. A tendency in some members of this stock to grow to larger size without much change in structure led, at the beginning of the Miocene, to the development of *Anchitherium*, about the size of a pony but with persistently primitive three-toed feet and low-crowned teeth. This type migrated to Europe (where true horses had been absent since the Eocene) and was common there in the early Miocene. Members of this group of relatively primitive forest horses persisted on into Pliocene times (one of them reaching China), despite the fact that other and more progressive horses were developing in the meantime. The larger forms of the late Miocene and Pliocene are often separated as a distinct genus—*Hypohippus*—and a giant form from the Pliocene, which may have been the size of an African rhinoceros, has been given the appropriate name of *Megahippus*. *Archaeohippus* repre-

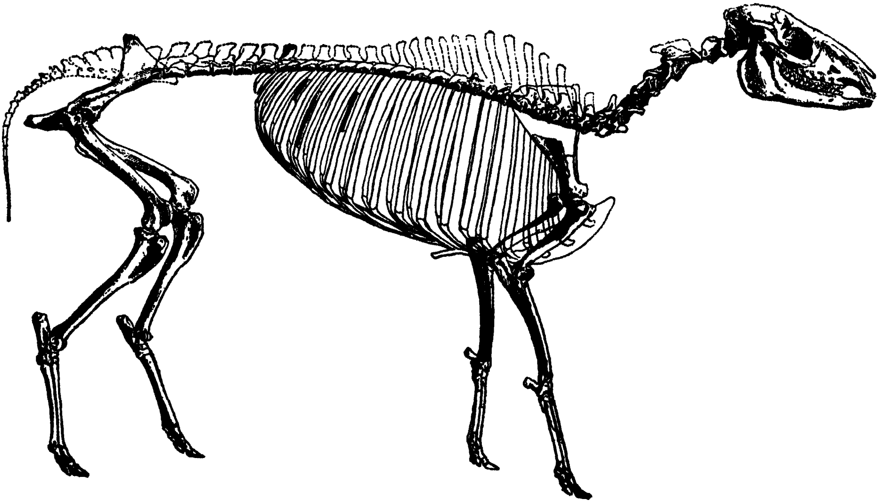


FIG. 325.—*Mesohippus*, a small, three-toed Oligocene horse, about 40 inches long. (From Scott.)

sents another series of conservative Miocene horses, which, however, were of very small size.

Miocene horses.—The beginning of a third main structural stage is found in *Parahippus* of the Miocene of North America. In this horse the diastema was well developed, and the molar teeth were lengthening. The face was consequently somewhat elongated, the orbit being considerably back of the middle of the skull length. The eye was partly inclosed behind by a developing process from the frontal; this formed a complete bar in all later types. While the molar teeth (Fig. 322, *C*) were still fairly low crowned, cement was beginning to make its appearance on their surfaces. In connection with this feature, a posterior ridge develops on the upper molars connecting the hypocone with the ectoloph, and a cross-connection (crochet) tends to connect protoloph and metaloph; these new structures result in the formation of "lakes" in the center of the tooth in which cement is deposited. In the feet the side toes were somewhat reduced, so that they would probably not have touched the ground during rapid locomotion. Thus, it would seem that in *Parahippus* we have a form transitional from the old forest dwellers to modern plains-dwelling grazing horses.

Directly descended from this genus was *Merychippus* (Figs. 319, *C;* 322, *D*), characteristic of the later Miocene of North America and the undoubted ancestor of the later horse types. Here the teeth were definitely high crowned and prismatic, with a good cement covering and a molar pattern quite comparable to that of living horses. The development of hypsodont teeth is usually regarded as associated with grass-feeding; this highly siliceous material would rapidly abrade low-crowned structures. This may well be the case. But we may note that Miocene horses were characteristically of larger size than their Oligocene predecessors. And simple mathematical considerations indicate that, even without change of diet, larger size would necessitate either larger grinding areas on the teeth or higher crowns.

Later horse evolution.—From *Merychippus* arose a variety of genera which comprise the horse fauna of the Pliocene; most had become extinct by the end of the Tertiary. *Hipparion, Neohipparion,* and *Nannippus* are a group of closely related forms of rather light build. *Hipparion,* about the size of a pony, spread through Asia to Europe (in which area *Anchitherium* had already disappeared), was characteristic of the Pliocene fauna there, and may have persisted in Africa with other relic types until the Pleistocene. *Neohipparion* and *Nannippus* (the last a small form) were confined to America, as was *Calippus*—a small relative of *Pliohippus.*

This last genus (Fig. 322, *E*) is the Pliocene American stock from which it appears that the modern horses and their relatives have come. There is a trend toward larger size, tooth patterns resembling those of living equids, and a rather stouter body build than in the *Hipparion* group. The feet are poorly known, but complete (if very slender) side toes were present in some forms. Some descendants of this group which reached South America became specialized types, such as *Hippidion* (Fig. 326) and *Onohippidium*. In these small but heavily built South American types, as in the true modern horses, the side toes were reduced to splints, but the limbs were short (suggesting a mountain habitat); and they differed in the excessively long and slim nasal bones. These forms did not survive the Pleistocene.

The major line of descent from *Pliohippus*, however, is that which led to the genus *Equus*, the living group of horselike animals. The rather slight remaining modifications, apart from the definite reduction of the side toes, appear to have taken place close to the Pliocene-Pleistocene time boundary; some of the transitional types occur in beds which are commonly considered as late Pliocene. For the most part, however, *Equus* is characteristically a Pleistocene genus, and its appearance is often considered as a time marker for that epoch. The genus appeared in North America but spread with remarkable rapidity to every continent (except, of course, Australia). Minor differentiations, hardly of generic worth, led to the development of the various modern horselike animals.) The earliest American horses and some of those present in the Pleistocene of Europe show features suggestive of the zebras, now confined to Africa. Other horse types are the asses still found wild in some of the more barren tropical regions, and the true horses, of which a wild species still exists in central Asia. Strangely enough, while North America had been, all through the Tertiary, the center of horse evolution, with only a few occasional migrants reaching Eurasia, the group had become extinct in the New World by the end of the Pleistocene. The American plains and pampas, which proved to be perfectly suitable for horses when reintroduced by man, were barren of equid life when first seen by Europeans.

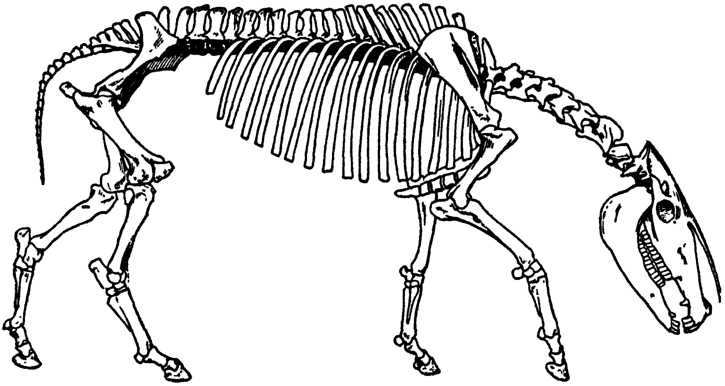


FIG. 326.—*Hippidion*, a South American Pleistocene horse. (From Scott, *Land Mammals of the Western Hemisphere*, by permission of Macmillan Co., publishers.)

Palaeotheres.—True horses, as we have noted, were absent in the later Eocene of Europe. Instead, we find developing various short-lived side branches of the equoid stock which may be considered collectively as the "palaeotheres." These forms tended to become prematurely large and advanced in structure. *Palaeotherium* (Fig. 327), which survived to the beginning of the Oligocene, may be taken as characteristic of the group. The last of the palaeotheres reached the size of a rhinoceros. The toes were reduced to three in both front and hind feet, but the legs were rather short and stout. Three premolars had become somewhat precociously molarized in the course of development of the genus; and the cheek teeth became markedly lophodont, although differing in details from those of the true horses. Other forms of Middle to Upper Eocene age were generally smaller, with somewhat more primitive teeth and less premolar development. One form, however, had already acquired cement on the molar crowns and had very slim lateral metapodials—features which were not attained in the true horses until the beginning of the Miocene. Despite these progressive features, the palaeotheres did not survive; the characteristic ungulates of the Oligocene and later Tertiary of Europe were artiodactyls, not perissodactyls.

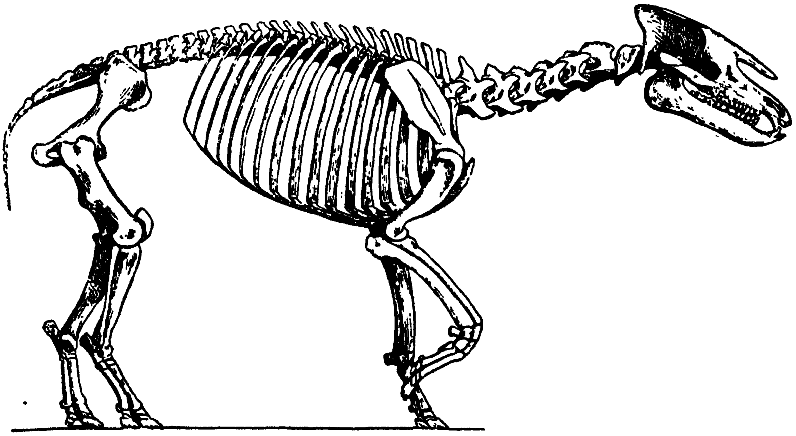


FIG. 327.—*Palaeotherium magnum*, a late Eocene giant horselike mammal, much reduced. (From Abel.)

Titanotheres.—Quite unlike the horses in their adaptations, but apparently closely related and derived from forms similar to *Hyracotherium*, were two extinct perissodactyl groups, the titanotheres and the chalicotheres. Both showed spectacular specializations but had an unprogressive dental equipment, a feature to which their extinction may be at least partially due. Of these two, the first to reach a climax and the first to become extinct were the titanotheres. This group had a major evolutionary center in North America, where they were present throughout most of the Eocene and into the early Oligocene. Until recently they were almost unknown in other parts of the world, but we now know a wealth of these forms from the late Eocene and early Oligocene of Asia as well; and late Eocene stragglers even reached eastern Europe. End-forms of the titanotheres are found in such genera as *Brontops* (Fig. 330), *Brontotherium*, *Titanotherium* [*Menodus*], and *Megacerops*, of the early Oligocene. These creatures were of great size, the height at the shoulder reaching 8 feet in one type. The skull (as in almost all titanotheres) was long and low; the brain was very small; and the braincase had a characteristic sag on top rather than any expansion of the skull. A striking feature was the development at the front of a pair of large, rugose, hornlike processes. These horns were always of fairly good size in these end-forms (although smaller in the females); but they varied enormously in the different genera, sometimes being long, diverging structures, sometimes (in *Embolotherium*, of the Oligocene of Mongolia) rising up sharply as a single broad, fused mass dividing at the top. The teeth (Figs. 320, *G;* 321, *E*), on the other hand, were strangely unprogressive. The incisors, as well as a premolar, might be lost entirely. The premolars were only partially molarized in pattern and small in size. The molars were large in surface area but crowned with a bunolophodont pattern. In the upper molars there was a W-shaped ectoloph like that of early equids, on the inner side of which lay the main grinding surface, and isolated internal cones representing protostyle, protocone, and hypocone. Below was a double V of somewhat the same pattern as that of the horses but without the reduplication of the cusp at the union of the V's which is found in most equids. The limbs, in correlation with the huge bulk, were of the graviportal type, short and massive with the conservative number of four and three toes, respectively, in the stubby front and hind feet (Figs. 328, *F;* 329, *D*).

In the Upper Eocene of America and Asia were somewhat more primitive types, such as *Dolichorhinus*, in which there were never more than slight traces of horns on the long nasal bones. In size the Upper Eocene types averaged but about two-thirds that of the end-forms; and the body was, in consequence, less massive in its proportions. All the teeth were present, the upper molars still possessed the two primitive intermediate cusps lost later, and the premolars were all simple and unmolarized. A further stage back is found in *Palaeosyops* and *Limnohyops* (Fig. 323, *G*), of the Middle Eocene of North America, which had reached only the size of a tapir and were hornless. In the late Lower Eocene there was present in North America not only a primitive true titanothere (*Eotitanops*) but also a small form, *Lambdotherium*, intermediate between titanotheres and the primitive equoid types.

The main evolutionary trends seen in this series of forms seem to point toward the rapid attainment of large size. The development of horns seems to have been a somewhat ineffective "attempt" at protection against the larger contemporary carnivores; it is to be noted that in Upper Eocene times rudimentary horns were developing independently in a number of separate lines of titanotheres. Lack of good brains and of good teeth seems to have been the main factor in their failure to succeed. Their diet must have consisted of extremely soft vegetation; for, despite the large amounts of food which must have been required for the sustenance of the huge body, the teeth could not undergo any great amount of wear. Any slight change in the vegetation and curtailment of soft food would readily have destroyed their hold on existence.

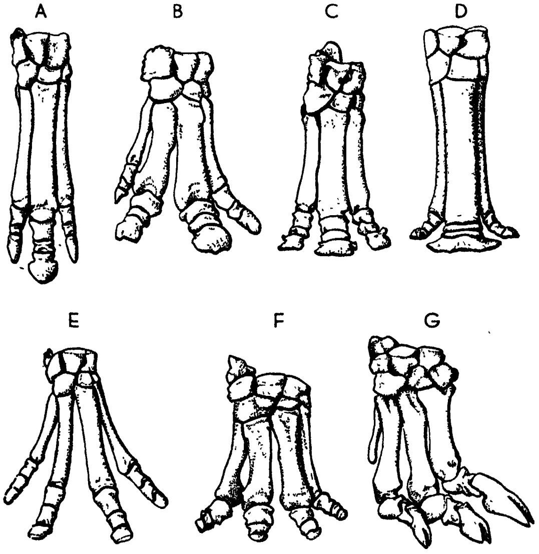


Fig. 328.—Manus of various perissodactyls. *A*, *Hyracodon*, an Oligocene running rhinoceros; *B*, *Trigonias*, an Oligocene four-toed true rhinoceros; *C*, *Diceratherium*, a three-toed primitive rhinoceros; *D*, *Baluchitherium*, a large Oligocene Asiatic rhinoceros with a pillar-like limb; *E*, *Protapirus validus*, an Oligocene tapir; *F*, *Titanotherium*; *G*, *Moropus*, a chalicothere. (*A* after Scott; *B* after Hatcher; *C* after Peterson; *D*, *F* after Osborn; *E* after Wortman and Earle; *G* after Holland and Peterson.)

Chalicotheres.—The characteristics of those most curious perissodactyls, the chalicotheres, are for the most part well illustrated in *Moropus* (Fig. 323, *H*), of the American Lower Miocene. In general appearance (as well as in size) *Moropus* was probably rather horselike, although the front legs were somewhat longer than the hind. The perissodactyl nature of this beast is indicated by many features of the skull and skeleton. In the slim skull the general proportions were those of the horses of that age; the long slender nasals were a perissodactyl character. The cropping teeth were weak or absent in chalicotheres. Unlike the typical perissodactyls, the premolars had remained comparatively small and simple; but the molars (which tended to remain low crowned) were rather similar to those of the titanotheres, with a double V in the lower molars and a W-shaped ectoloph above (Figs. 320, *H;* 321, *F*).

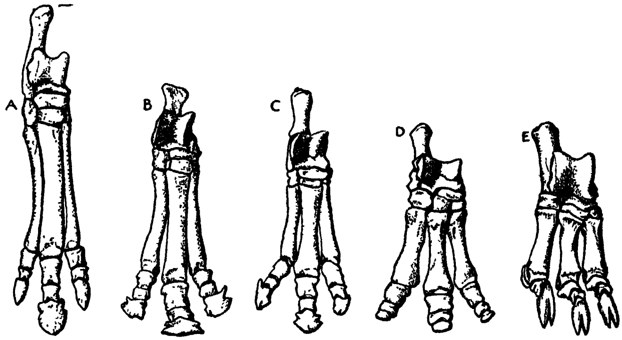


FIG. 329.—The pes of various perissodactyls. *A*, *Hyracodon*, an Oligocene running rhinoceros; *B* *Diceratherium*, a Miocene rhinoceros; *C*, *Protapirus*; *D*, *Titanotherium; E*, the chalicothere *Moropus* (*A* after Scott; *B* after Peterson; *D* after Osborn; *E* after Holland and Peterson.)

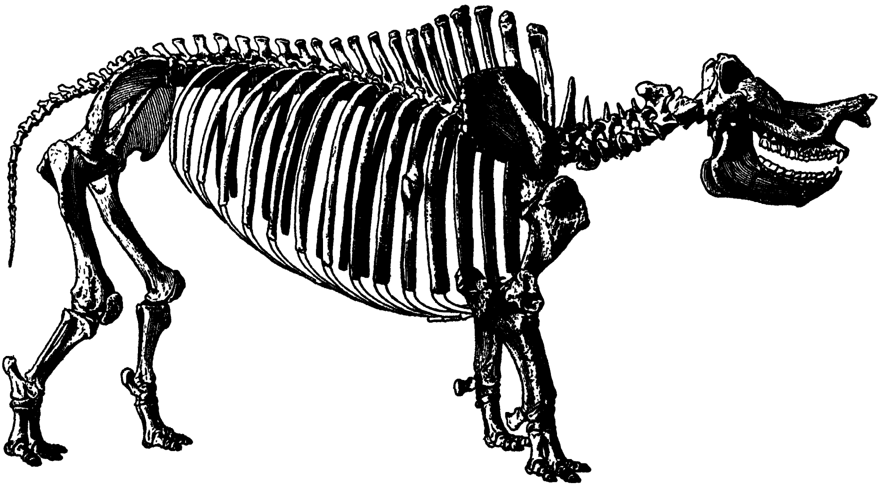


FIG. 330.—*Brontops*, a large Lower Oligocene titanothere. The specimen figured is a female, the short horns being a sex difference; original about 14 feet long. (From Osborn.)

In the feet (Figs. 328, *G;* 329, *E*) we have quite another story. There were in this genus three toes in each foot, and the manus was primitive in retaining a well-developed metacarpal for a small fifth digit (lost in other perissodactyl groups by that date). So far all is still orthodoxly perissodactyl. But the digits, instead of bearing hoofs, were terminated by large fissured ungual phalanges, undoubtedly bearing not hoofs but stout claws.

Such a feature is one quite unlooked for in a form which otherwise agrees so well with the hoofed groups considered in this chapter; for half a century or so after the first fragmentary remains of chalicotheres were discovered it was not imagined that skull and feet could possibly have pertained to the same form. Because of the claws, some are inclined even today to place these chalicotheres in a separate order or suborder.

But the rest of the skeleton is so typically perissodactyl that we cannot refuse them admittance to this group. We must regard them as a specialized side branch of the perissodactyls in which the high development of claws is associated with some specialized habit of these forms. The long front legs of *Moropus* and other members of the chalicotheres have suggested to some a browsing habit in which the front feet may have been used in dragging down branches. But a more probable explanation is that the food consisted of roots and tubers and that the claws were used as digging organs.

Older forms were present in the Eocene and Oligocene of both Eurasia and North America. The Eocene *Eomoropus* had attained only the size of a sheep and had (as usual in Eocene perissodactyls) a well-developed fifth finger and even a vestige of the pollex, unknown in other perissodactyls. The ungual phalanges show little of the later compression into claw-bearing organs, and the dentition was unreduced and quite primitive. This form was not far from the common perissodactyl stock.

While the Middle Miocene saw the extinction of this group in America, chalicotheres persisted much later in Eurasia, with forms in the Miocene and Pliocene, such as *Chalicotherium*, in which the front legs were much longer than the hind. Chalicotheres continued on into the Pleistocene in eastern and southern Asia and in Africa; but, despite this late persistence in the tropics, the group finally became extinct.

Tapirs and related types.—It has become clear in recent years that if the perissodactyl families be grouped into larger categories, one major assemblage should include (despite their diversity in appearance) the forms considered up to this point; a second group should comprise the tapirs and rhinoceroses and their extinct kindred. One feature indicative of this dichotomy is to be found in the construction of the upper molars (Fig. 320; cf. *A*, *B*, *G*, *H* with *C–F*). Horses, titanotheres, and chalicotheres early acquired a powerful W-shaped ectoloph, and transverse ridges are either slow to appear (as in equids) or fail to develop at all. In the tapir-rhinoceros group, in contrast, the ectoloph is a simple structure, and emphasis is laid on the development of transverse protoloph and metaloph.

Primitive living representatives of this latter group and forms which are still very close in many respects to the common ancestors of all perissodactyls are the tapirs (*Tapirus*) of tropical America and the oriental region. Living in forest regions and on comparatively soft ground, they have persistently retained the primitive limb structure of their Eocene ancestors: the legs and feet (Figs. 328, *E;* 329, *C*) are short; ulna and fibula are still complete and unfused; and, as in the Eocene perissodactyls, there are four toes in the front foot and three behind. The tapirs are still browsers, with low-crowned teeth which have no cement covering. The canines are well developed, and there has been no loss of teeth, although a moderate diastema is developed. The modern forms have molarized three premolars, as have the horses. All the cheek teeth (Figs. 320, *E;* 321, *D*) have a very simple pattern, the upper molars having a pattern of simple lophs while the lower teeth have developed two cross-crests. The one noteworthy specialization of the modern tapir is the presence of a short proboscis, with the accompanying backward migration of the bony opening of the nose and shortening of the nasal bones found in all forms which have developed a trunk (Fig. 323, *F*).

True tapirs appeared, as the genus *Protapirus*, in the Oligocene of both Europe and North America. A number of Tertiary genera have been described, but all are very close to the modern type, and generic distinctions are slight. Specimens are few, presumably in relation to the forest-dwelling habits of the family, but (except for an absence of evidence of Pliocene American forms) they persisted in the present north temperate regions of both hemispheres until the Pleistocene. With the climatic vicissitudes of this last epoch they became restricted to the tropics. In the Old World their final refuge has been the Malayan region; in the New, they successfully invaded South America.

Although the tapirs in a narrow sense are not found before the Oligocene, there are numerous tapir-like forms in the Eocene, of which *Homogalax* (Fig. 320, *F*), *Lophiodon*, and *Heptodon* are representative. These are sometimes grouped as "lophiodonts" but are currently thought better arrayed in three separate, but related, small families. The cheek teeth are of simple lophodont structure, with little of the molarization of the premolars seen in modern tapirs. Some of these genera may be close to the ancestry of true tapirs; others may be closely related to ancestral rhinoceroses; a majority, however, appear to represent short, sterile twigs of the perissodactyl family tree. Most were of rather modest size, but *Lophiodon* of the late Eocene of Europe was as large as a modern rhinoceros. This form was of ponderous build; others were more slender-legged, paralleling the early horses.

Rhinoceroses.—Among all the perissodactyl groups, the most complicated fossil history is that of the Rhinocerotoidea, the rhinoceroses and their relatives. At present there survive of the rhinoceroses only a few forms in the Old World tropics, but throughout most of the Tertiary they were exceedingly numerous in the northern continents. Starting from forms rather similar to the early tapirs, they have tended to diverge considerably from that group. In many cases there have developed hornlike structures, which, however, are composed, not of bone or horn, but of a fused mass of modified hair. As contrasted with most equids, rhinoceroses have tended to grow to large size, usually with comparatively short, stout limbs in which digital reduction has proceeded at a slow pace, for the fifth digit in the hand was present in some Oligocene forms, and a monodactyl stage has never been attained. The premolars have tended to molarize, but the row of cheek teeth does not greatly lengthen, and the face is usually comparatively short. The molars have a comparatively simple π-shaped pattern above, and in all later forms the last molar is reduced; the lower molars develop two asymmetrical crescents. The cheek teeth seldom tend to become very high crowned, and cement is almost never present. The incisors and canines, however, are variable, and there are frequent losses and specializations.

Running rhinoceroses.—The rhinoceroses are currently divided into four families, the two more primitive of which—the Hyrachyidae and Hyracodontidae—are frequently termed "running rhinoceroses." *Hyrachyus* (Figs. 320, *C*; 323, *C*) and a few closely related forms from the North American Eocene were similar to the Eocene horses in build and still more similar to the tapiroid genera discussed above; the various species ranged in size from the dimensions of a wolfhound to those of a mustang. The complete dentition was present; but, while the essential features of the rhinoceros molar pattern were developed, the premolars were still simple and not molarized; the incisors were unspecialized, and canines were well developed. The legs were slim and rather like those of *Eohippus*, with four toes in front and three behind; the neck, in contrast with most later rhinoceroses, was long.

A second type of running rhinoceros is found in *Hyracodon* (Figs. 328, *A*; 329, *A*; 331) of the North American Oligocene and its forerunners in the late Eocene of both North America and Asia. This genus was of rather large size, with the cheek teeth much more typically rhinocerotic and with the back premolars already molarized. *Hyracodon* was somewhat more specialized for a cursorial life than *Hyrachyus*, with long, slim legs and but three toes on front as well as hind feet. These evolutionary advances were very similar to those found in the contemporary horses but were not continued, for the group disappeared before the close of the period, perhaps because of unsuccessful competition with these rivals.

Amynodonts.—An early side branch, presumably derived from the primitive hyracodonts, was that of the family Amynodontidae. These forms are found in the late Eocene and Oligocene of both Eurasia and America and persisted in Asia until the Miocene. They had about the general size and proportions of a hippopotamus, and the conditions under which their remains are found suggest that they were river-living forms. *Metamynodon* (Fig. 332) of the American Oligocene had short, massive limbs, still retaining four short toes in front and three behind. In the short, heavy skull the premolars had failed to molarize, several had been lost, and the incisors were also reduced; on the other hand, the canines and molars were much enlarged.

Early true rhinoceroses.—All remaining forms are commonly placed in a fourth family as true rhinoceroses, the Rhinocerotidae. It seems certain that these types were derived from early running rhinoceroses, but Eocene forerunners are represented by only a few questionable or poorly known types. The true rhinoceroses first became prominent in the Oligocene and (in contrast with the contemporary running rhinoceros) tended to large size and stout limbs, while (in contrast with the amynodonts) the premolars became rapidly molarized. The cropping mechanism of true rhinoceroses is peculiar: a pair of incisors, the first upper and second lower, are always enlarged cutting teeth (in some late forms they may be secondarily lost), and a narrow muzzle with a pointed lip develops. The last upper molar is always simpler than the others, with ectoloph and metaloph forming a single continuous crest (Fig. 320, *D*).

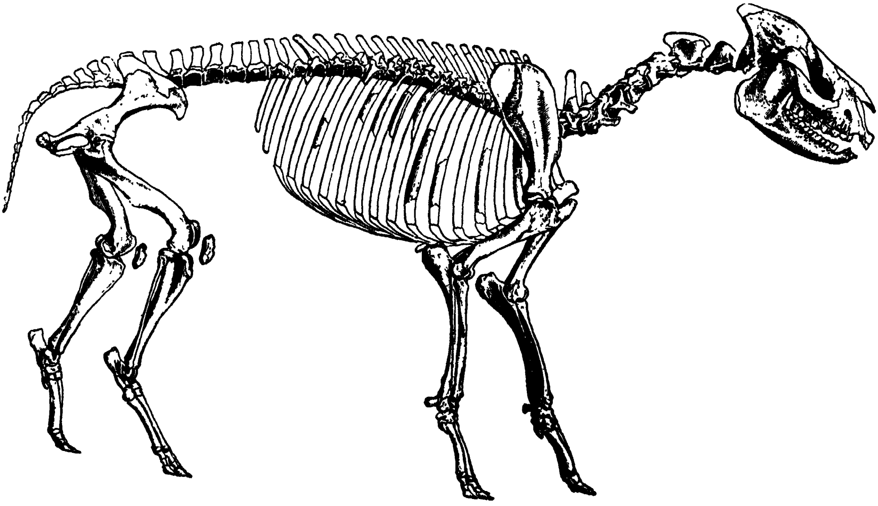


FIG. 331.—*Hyracodon*, an Oligocene running rhinoceros, about 5 feet in length. (From Osborn.)

Trigonias (Fig. 328, *B*), *Subhyracodon*, *Caenopus* (Fig. 333), and related forms from the Oligocene of North America and Europe appear to represent the central stock of the true rhinoceroses. *Caenopus* had already attained fairly large size (the skull averaged well over a foot in length), and the limbs supporting the stocky body were stouter and shorter than in the hyracodonts and comparable to those of modern tapirs. Four toes were still present in front in *Trigonias*, but the fifth toe was already small and had disappeared in *Caenopus*. All later types retained a three-toed foot. Incisor tusks were developed; and most of the other front teeth were retained, in contrast with later forms. The premolar teeth were at first simple but during the Oligocene tended to assume the molar pattern. The primitive Oligocene rhinoceroses were hornless (the matted hair of the "horn" fossilizes in relatively few cases, and our evidence for the presence of a horn usually consists of a roughened area on the skull for its attachment).

A number of later Miocene and Pliocene genera, such as *Aceratherium* of Eurasia and certain rarer American contemporaries, show relatively little change from the primitive pattern. These forms exhibit a tendency toward incisor reduction, but there is little evidence of horn development or other specializations.

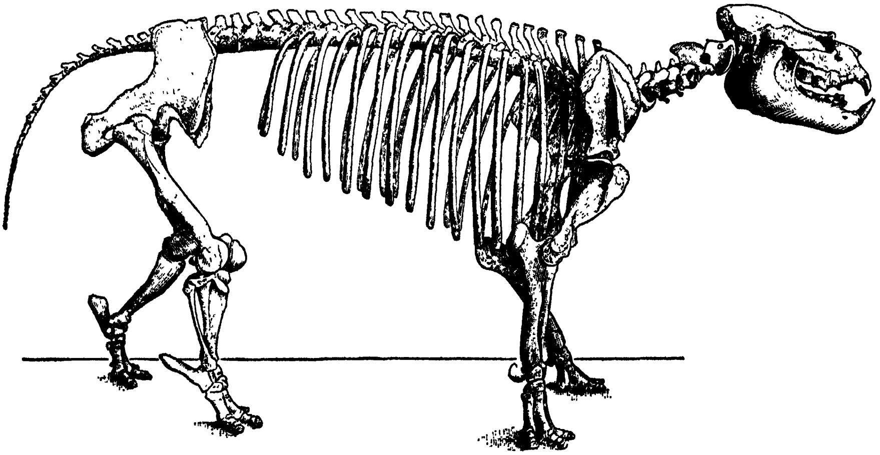


FIG. 332.—*Metamynodon*, an Oligocene amphibious rhinoceros (Amynodontidae), about 14 feet in length. (From Osborn.)

The evolutionary history of the rhinoceroses offers a strong contrast to that of the equids. In the horses we have seen that there was a main stem on the evolutionary tree with but a few short side branches; rhinoceros evolution, on the other hand, may be pictured as a branching bush. There is no main evolutionary stem, but a complex of sprouts, the components of which are difficult to disentangle.

An early branch from the *Caenopus* stock is that represented by *Diceratherium* of the American Miocene. This genus was quite similar to its Oligocene ancestors except for the fact that the males possessed small horns; but, unlike those of other later horned rhinoceroses, these horns were placed side by side at the tip of the nose.

Giant rhinoceroses.—Equally prompt to appear was a much more spectacular and aberrant group including *Baluchitherium* (Fig. 323, *D*) and related huge hornless forms from the Oligocene and early Miocene of Asia. These were the largest of known land mammals. The head of *Baluchitherium* was about 4 feet in length but, even so, was small in proportion to the body size. This great beast must have stood about 18 feet high at the shoulders, with a long neck which, combined with long front legs, enabled him to browse on the higher branches of the trees. The grinding teeth were like those of *Caenopus*, while the single pair of blunt incisors, which were his only front teeth, are easily derivable from those of the more primitive Oligocene forms. The limbs, as would be expected, were massive but long, and pillar-like. There is even considerable elongation of the metapodials, which were stout and placed close together in a pillar above the three stubby toes (Fig. 328, *D*); the lateral digits were more reduced than in any other rhinoceroses.

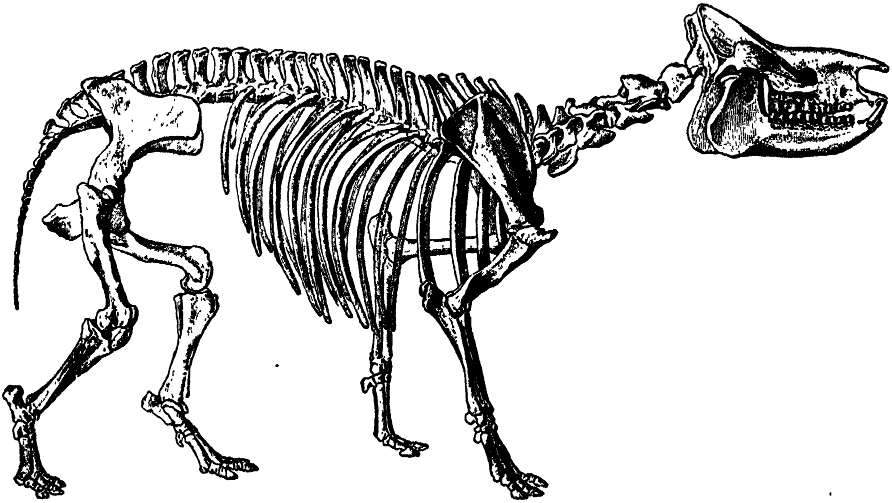


FIG. 333.—*Caenopus tridactylus*, an Oligocene hornless rhinoceros, about 8 feet in length. (From Osborn.)

Later rhinoceros types.—Beyond the Oligocene, rhinoceroses became relatively rare in America and died out during the Pliocene; in Eurasia, on the other hand, there are numerous and varied genera in Miocene, Pliocene, and even Pleistocene deposits. The various phyletic lines are incompletely established; however, at least five end-types can be distinguished and are listed below.

1. The short-legged rhinoceroses, such as *Teleoceras* and its relatives of the Miocene and Pliocene. These are round-bodied, stubby-limbed, and broad-footed beasts with a build like that of a hippopotamus and presumably similar amphibious habits. Technically they were horned, for there is a rugose area indicating the presence of at least a rudiment of this structure at the tip of the nasals. Alone of all the groups mentioned in this section, these rhinoceroses penetrated into North America, where abundant remains of *Teleoceras* have been found in early Pliocene deposits.

2. The term *Rhinoceros* in a narrow sense is confined to the large Indian "unicorn" and a smaller relative from Java, in which there is a single massive horn on the nasal bones and both incisor tusks have been retained. There are forms presumably ancestral in the later Tertiary of Eurasia.

3. Resembling the Indian rhinoceros in a single-horned condition but differing in the loss of incisors and other features, was *Elasmotherium* of the Pleistocene of the northern plains regions of Eurasia. This was a very large mammal; a great swelling, nearly a foot in diameter, on the frontal bone suggests the presence in life of a huge horn on the forehead. The name refers to the fact that the teeth, although possessing the basal rhinoceros pattern, have a wavy, straplike outline of the enamel. A Pliocene Asiatic form of simpler structure and smaller size appears to be ancestral.

4. *Dicerorhinus* of Sumatra is a two-horned rhinoceros; but, in contrast to the early diceratheres, the horns are here placed one behind the other, tandem fashion, and in the living form are of small size. This form has retained incisor tusks. Recent research indicates that the Pleistocene *Coelodonta* is related to the Sumatran form. This was the woolly rhinoceros of northern Eurasia, adapted to a cold climate. Of it we know far more than the skeleton; it was a favorite subject for Old Stone Age artists, and specimens "embalmed" in a waxy material in an oil seep have been discovered in Galicia. Ancestors of these Eurasian tandem-horned rhinoceroses have been traced back through the Tertiary to Oligocene times.

5. A final group is that of the African tandem-horned genera, the living "white" (*Ceratotherium*) and "black" (*Diceros*) (Fig. 323, *E*) rhinoceroses of Africa. In contrast to *Dicerorhinus*, the horns are much elongated and incisors are absent. Their exact ancestry is uncertain; it is possible that they developed in Africa, and our knowledge of fossil rhinoceroses from that continent is extremely limited.

The history of the rhinoceroses has, in general, run a course parallel to that of the related horses but with emphasis on bulk rather than on speed. Eocene and early Oligocene members of both groups tended to vary widely, producing in the case of the rhinoceroses not only running types but the large amynodonts. In the Oligocene the rhinoceroses, in the main, settled down to become a group of forms characteristically much larger than the horses but more conservative in that most remained browsing forms. Like the horses, they were abundant in late Tertiary and Pleistocene times but are now limited to a few Old World types.

With the rhinoceroses we terminate our account of the perissodactyls. All five main groups had appeared early in the Eocene, and during the early part of the Tertiary they flourished greatly. By the Miocene, however, they were beginning to lose somewhat in relative importance. In Pleistocene times horses and rhinoceroses still flourished. Today the perissodactyls are but an insignificant part of the world's ungulate population.

CHAPTER 23

ARTIODACTYLS

THE order Artiodactyla—the even-toed ungulates—includes a great variety of living hoofed mammals, such as the pigs and peccaries, hippopotami, camels, deer, cows, sheep, goats, antelopes, and their relatives, together with many important extinct types. Exceeded in numbers in early Eocene formations by the perissodactyls, they have succeeded in far outdistancing their rivals and are the dominant hoofed mammals of later Tertiary and Recent times.

Structure.—The most obvious and characteristic feature of the group is the type of toe reduction; for, whereas almost all other ungulates tend to have a mesaxonic foot with the axis through the third toe, the artiodactyls are paraxonic, with the axis between the third and the fourth toes. Pollex and hallux are rarely found, even in early forms. Four-toed types are common in the earlier part of the Tertiary; the pigs and hippopotami are still four-toed, and vestigial lateral "dew claws" are present in many other forms. The higher types tended early to reduce the toes to two on each foot, giving the typical "cloven hoof" in which the two principal metapodials fuse together into a cannon bone.

In contrast with perissodactyls, there is no third trochanter on the femur. The ulna is reduced and in higher forms fuses with the radius; and the fibula, too, is usually incomplete or fused with the tibia. In the carpus the three proximal elements are always separate, but in the distal row the magnum and trapezoid fuse in some advanced types to support the third metacarpal, while the unciform supports the fourth. The astragalus (Fig. 286, *C*) is the most characteristic bone in the skeleton, for it has not only a rolling surface above but an equally developed lower pulley surface, giving very great freedom of motion to the ankle. The astragalus rests equally on the navicular and the cuboid (these two elements are fused in many types [cf. Fig. 350]). The cuboid lies above the fourth toe, the outer of the two principal digits, while the navicular transmits half the weight to the third toe through the ectocuneiform (the other cuneiform bones tend to be reduced).

The dentition was complete in many of the early types, as it is still in the pigs. The most primitive forms known had normal incisors and rather large, carnivore-like canines. The premolars were simple, and the molars in the simplest forms were of the primitive tritubercular pattern with rather bunodont cusps. From this primitive pattern, not so different from that of primitive carnivores, there have been great variations.

The incisors are often reduced; and the upper ones are absent in the more advanced types, their place as a cropping organ being taken functionally by the gums over the premaxillae. The upper canines often form defensive tusks; the lower ones sometimes take on the aspect of incisors. A diastema has usually developed, and the first premolar is frequently absent. The premolars, in contrast with those of perissodactyls, do not usually assume the full molar pattern but remain comparatively simple (cf. Fig. 336). The cheek teeth, primitively low crowned, have become hypsodont in many forms. As in other herbivores the molars (Fig. 337) almost always take on a four-cusped pattern. The rather bunodont primitive condition may be emphasized, as in the pigs; but usually each cusp develops into a crescent, giving the typical selenodont pattern of the higher artiodactyls. In this process the outer cusps tended to become crescentic before the inner ones, giving a buno-selenodont condition in some fossil forms.

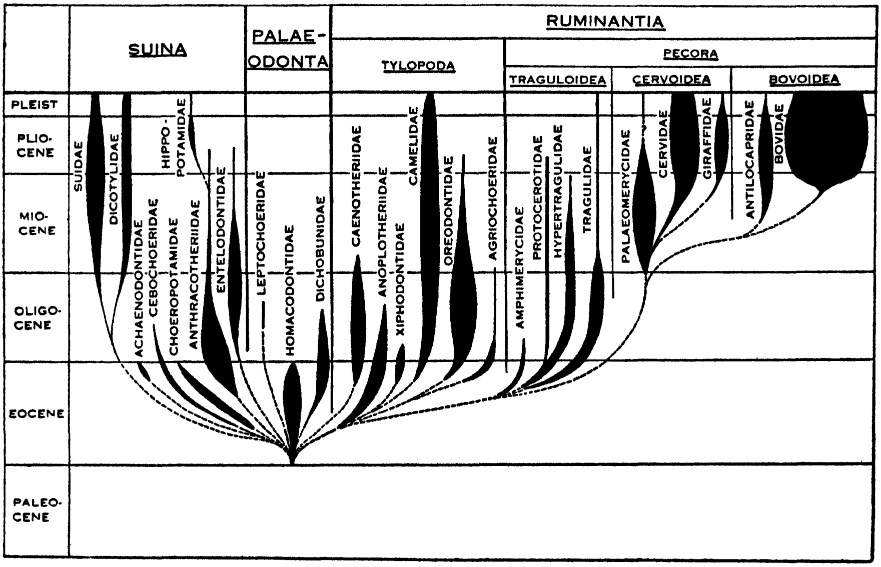


FIG. 334.—Provisional phylogeny of the artiodactyl groups

One peculiar feature, however, is found in the upper molars. In most mammals the posterointernal cusp of a four-cusped molar is obviously the hypocone. A hypocone is present in a few early artiodactyls (Fig. 337, *B*), but in the great majority of the group (including all living forms) it seems probable that the posterointernal cusp is not the hypocone but an enlarged metaconule and that the hypocone has never developed. In most Eocene forms we find five-cusped teeth, with protocone, protoconule, and paracone in the front half and metaconule and metacone in the posterior half of the tooth (Fig. 337, *C*, *H*, *K*). Toward the end of the Eocene the protoconule disappears in most lines, leaving protocone, paracone, metaconule, and metacone as the four definitive cusps (Fig. 337, *E–G*, *J*, *L–P*).

There are typically nineteen thoracic and lumbar vertebrae. The clavicle is, as might be expected, rarely present.

Many forms have a postorbital bar, and there is always at least a postorbital process. The front part of the skull is sharply bent down on the braincase in some advanced forms; the frontals tend to be large, the parietals, on the contrary, reduced. There are interesting variations in the development of the mastoid region (Fig. 335). In primitive mammals this region of the ear ossification appears to have been well exposed on the surface of the skull at the posterolateral corner of the braincase, between the exoccipital and the squamosal. This is still the case in living ruminants; but in the "swine" the squamosal has grown back to meet the exoccipital over the area once occupied by the mastoid, and this last no longer reaches the surface.

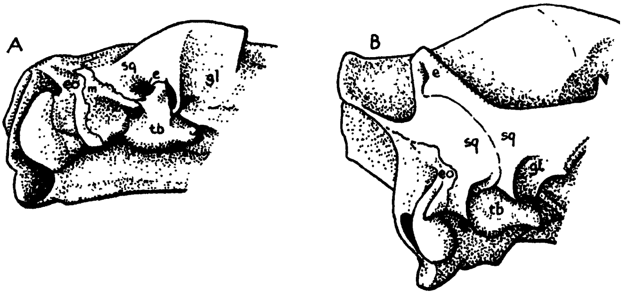


FIG. 335.—Lateral (and somewhat ventral) views of the posterior part of the skull in *A*, the anoplothere *Diplobune*, and *B*, the peccary *Dicotyles*, to show the contrast between mastoid and amastoid artiodactyls. In *A* the mastoid is widely exposed on the surface of the skull between the squamosal and the exoccipital; in *B* this area is occupied by an extension of the squamosal. Abbreviation: *e*, external auditory opening; *eo*, exoccipital; *gl*, glenoid cavity; *m*, mastoid; *sq*, squamosal; *tb*, tympanic bulla. (After Pearson.)

Classification (cf. Fig. 334).—The artiodactyls appear in the fossil record at the beginning of true Eocene times. These earliest types were quite primitive in many respects, with simple teeth implying a mixed diet and with features which suggest a relationship to the primitive carnivores. Nevertheless, such distinctive artiodactyl features as the double-pulleyed astragalus were already developed, and it is obvious that the ancestral forms must have been undergoing development in some unknown area in Paleocene times.

Inconspicuous at the beginning of the Eocene, the artiodactyls had developed into a great variety of types by the end of that period. Many of these have since become extinct, but others are indicative of the lines of descent leading to the existing forms.

The classification of living artiodactyls is simple. They comprise: (1) the suborder Suina, or swine in a broad sense—pigs, peccaries, and hippopotami; (2) the suborder Ruminantia, cud-chewers, which include (*a*) the Tylopoda, or camels, and (*b*) the Pecora, the deer-giraffe-antelope-cattle group; the little chevrotains (tragulids) of the Old World tropics are sometimes treated as a separate group, sometimes (as here) considered to be primitive pecorans.

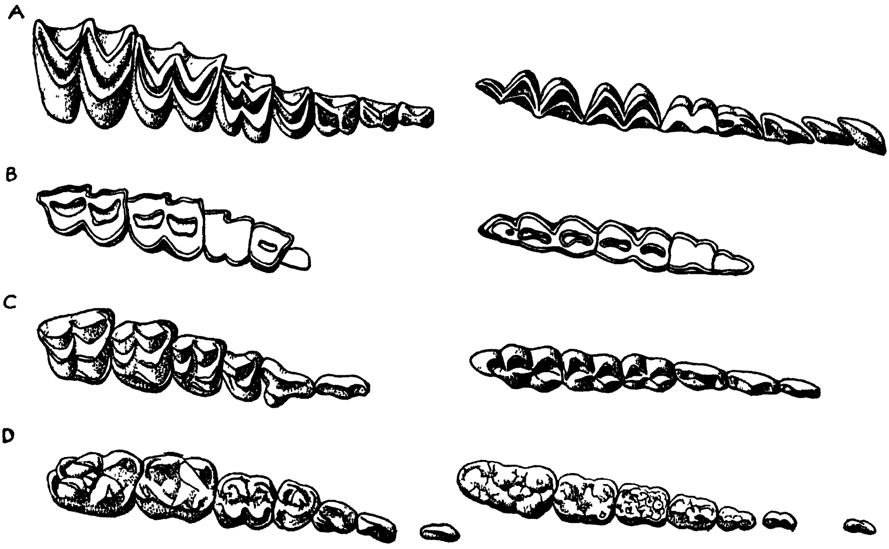


FIG. 336.—The cheek teeth of artiodactyls. *Left*, teeth of upper right side; *right*, teeth of lower left side. *A*, *Merycochoerus*, a Miocene oreodon, ×$\frac{1}{3}$ approx.; *B*, *Camelops*, a Pleistocene camelid, ×$\frac{2}{7}$; *C*, *Archaeomeryx*, a primitive fossil pecoran, ×$\frac{3}{2}$ approx.; *D*, *Chleuastochoerus*, a Pliocene pig, ×$\frac{2}{5}$. (*A* after Loomis; *B* after Merriam; *C* after Matthew; *D* after Pearson.)

The "swine" have bunodont molar teeth, canine tusks, four-toed feet with separate metapodials in most cases, a simple stomach, and a concealed mastoid region. The living ruminants have selenodont molars; the upper incisors are small or absent; the upper canines are sometimes enlarged in males as weapons but are usually reduced or lost; the feet are usually two-toed, with a cannon bone; there is a compound ruminating stomach; and the mastoid is exposed on the surface.

But when the fossil forms are included, such an easy separation is impossible; we are confronted with a large array of families which are intermediate in many respects between existing types or belong to extinct side branches.

The various classifications that have been made vary greatly. This reflects the fact that in the early artiodactyls the features of teeth, skull, and feet which are useful in distinguishing the two major existing groups were present in variable and confusing combinations. However, when the Eocene forms are viewed broadly, it becomes evident that the forms present were, for the most part, tending in two major directions: on the one hand, toward types with bunodont dentitions, incisors, and canines of primitive type and an "amastoid" ear region and, on the other, toward animals with selenodont cheek teeth, modified front teeth, and a persistently exposed mastoid region. We are thus justified in adhering essentially to the type of classification used for modern forms in making a major division into two suborders, Suina and Ruminantia, although adding a third category, Palaeodonta, for certain early and primitive types close to the point of origin of the order.

Archaic artiodactyls: the palaeodonts.—An assemblage of small artiodactyls from the Eocene and early Oligocene (mainly in North America) is that including such genera as *Diacodexis* and *Homacodon* of America and the European *Dichobune*. Many are inadequately known, and there is some variety in their structure, but this group includes the oldest and seemingly the most primitive of known artiodactyls. They are in many respects close to the primitive placental stock; and, were it not for the discovery in some instances of a typical artiodactyl astragalus associated with them, their position as artiodactyls (rather than insectivores or primates) might be questioned. There are few remains of the postcranial skeleton, but the limbs appear to have been generally short and primitive, with four functional toes and presumably a small pollex in some forms. The skull, as seen in *Homaco-*

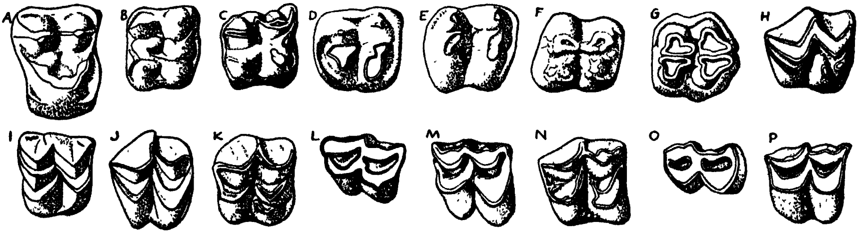


FIG. 337.—Right upper molar teeth of artiodactyls. *A*, *Diacodexis*, a Lower Eocene form with tritubercular molars; *B*, *Dichobune*, a hypocone present, in contrast with most members of the order; *C*, *Anthracotherium*, a bunoselenodont, five-cusped molar; *D*, *Archaeotherium*, an entelodont, with a piglike tooth but hypocone developed; *E*, *Platygonus*, a peccary; *F*, *Sus erymanthus*, a Pliocene pig; *G*, a Pleistocene *Hippopotamus*; *H*, *Anoplotherium*, a bunoselenodont type with protoconule still present; *I*, *Caenotherium*, with protocone migrated to back half of tooth; *J*, *Oreodon*, a simple, four-cusped selenodont tooth; *K*, *Xiphodon*; *L*, *Alticamelus*, a Pliocene camel; *M*, *Samotherium*, a Pliocene giraffe; *N*, *Dicrocerus*, a primitive deer; *O*, *Tetrameryx*, a Pleistocene prongbuck; *P*, *Tragocerus*, a Pliocene bovid. (*A* after Sinclair; *B*, *I* after Stehlin; *C*, *F*, *H*, *P* after Gaudry; *E* after Osborn; *G* after Cuvier; *K*, *N* after Schlosser; *L* after Cook; *M* after Ringström; *O* after Lull.)

don (Fig. 343, *A*) was low and moderately elongate, and it is probable that the mastoid was generally exposed in primitive placental fashion. The molar teeth in the earlier Eocene genera were neither markedly bunodont nor markedly selenodont but showed a pattern of moderately blunt cusps; selenodont tendencies appear in most later genera. In *Diacodexis* (Fig. 337, *A*) the upper molars are still in the primitive tritubercular stage seen in many Paleocene mammals; and this condition persists in a few rare Oligocene forms, such as *Leptochoerus*. However, the group here considered differs from nearly all other artiodactyls in that some later Eocene and early Oligocene forms developed a hypocone, giving a six-cusped tooth (Fig. 337, *B*) in the fashion of "normal" placentals and in contrast with more characteristic artiodactyls. *Homacodon* and other American types retained primitively enlarged canines, as in the later swinelike artiodactyls; *Dichobune*, on the other hand, reduced its canines so that its teeth form a rather uniform and continuous row, as in many early ruminants.

The late Eocene and Oligocene members of this archaic assemblage appear to be end-forms, without descendants; the earlier Eocene genera, however, may well be the true ancestors of later artiodactyls. How to classify them formally is a problem without any satisfactory solution; they are neither good swine nor good ruminants. One solution, adopted here, is to place them in a separate basal artiodactyl group as the suborder Palaeodonta.

Primitive swine.—In the suborder Suina we shall here treat of the pigs, peccaries, hippopotami, and a number of fossil groups which may be associated with them. In almost none of these forms is there any development of a selenodont pattern in the teeth; on the contrary, there is usually a highly developed bunodont condition. The limbs are short and quite primitive in nature, generally with four well-developed toes. A cannon bone is almost never formed, and the lower leg bones (in contrast to higher ruminants) almost always remain separate. The stomach is always simple, and the diet of the swine is a mixed one. In typical members of the group the skull shows an amastoid condition. Applying these diagnostic characters to fossil types, we find that in the Suina, in a broad sense, we may include not only the surviving groups mentioned but also the entelodonts or "giant pigs" and the anthracotheres, both prominent in Middle Tertiary faunas.

The Suina are first seen in the Eocene in forms which presumably arose from members of the palaeodont stock. In the middle and later Eocene there are various genera which show evidence of a trend toward characteristic features of the suborder. The teeth are definitely bunodont and often show a pattern of five cusps (reduced in most cases to four at about the end of the period); the canines remain prominent; most show an amastoid condition. Some, like *Achaenodon* (Fig. 338, *A*) and *Cebochoerus*, are short-faced forms which have left no known descendants. Others, such as *Helohyus* and *Choero-*

potamus, are longer faced and may as a group be ancestral to the characteristic Suina of later periods.

Entelodonts.—One offshoot of the primitive "swine" stock which early rose to prominence and early disappeared was the family Entelodontidae, the "giant pigs" which flourished in Oligocene times. Common Oligocene genera were *Entelodon* in Europe, and the similar *Archaeotherium* (Figs. 337, *D;* 338, *B*) in America. Last and largest of the group was *Dinohyus* (Figs. 342, *C;* 339) of the early Miocene of America. The entelodonts were large

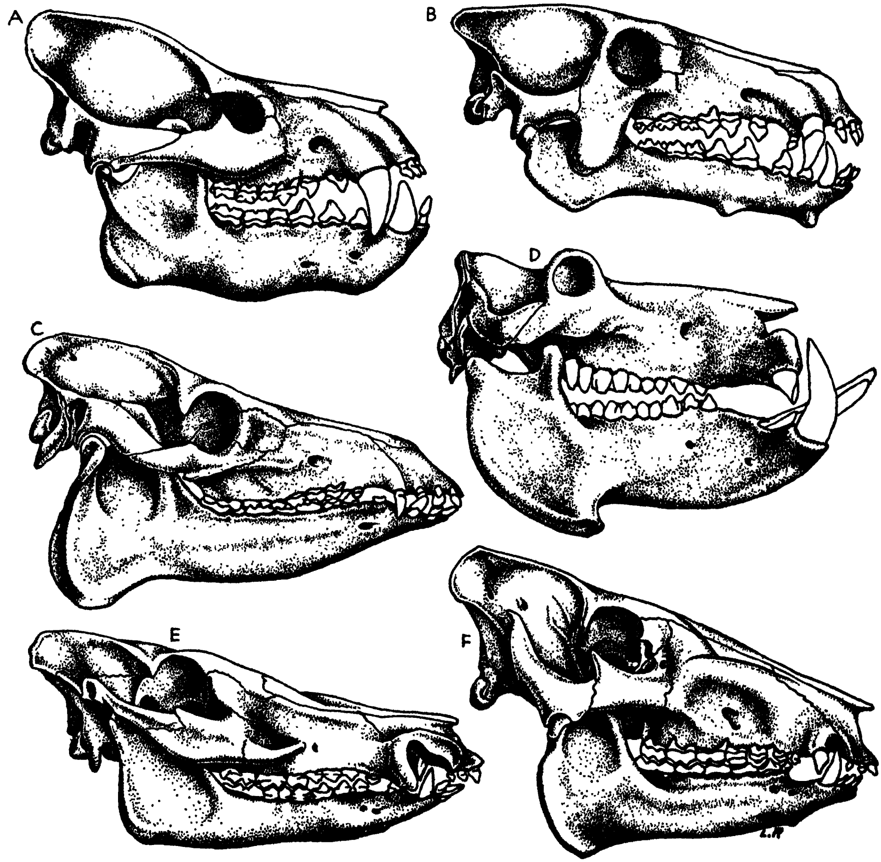


FIG. 338.—Skulls of piglike artiodactyls. *A*, *Achaenodon*, an upper Eocene "short-faced pig," skull length about 15 inches; *B*, *Archaeotherium*, an Oligocene entelodont, average skull length about 18 inches; *C*, *Bothriodon*, an Oligocene anthracothere, length of skull about 17 inches; *D*, a Pleistocene European *Hippopotamus*, skull length about 2 feet; *E*, *Chleuastochoerus*, a late Tertiary pig from China (boar), skull length about 12 inches; *F*, *Perchoerus*, an Oligocene and Miocene peccary, skull length about 10½ inches. (*A*, *F* after Peterson; *B*, *C* after Scott; *D* after Reynolds; *E* after Pearson.)

forms, with huge skulls often reaching nearly a yard in length. The incisors were long and pointed; the canines, heavy and showing wear-grooves suggesting a root-eating diet. The premolars were simple; the molars were relatively small, with bunodont cusps. In the upper molars there is thought to be a true hypocone, which we have noted as found elsewhere only in some very primitive forms. The skull was much elongated, especially the facial region, while the braincase was small; a postorbital bar had already developed. A large flange was present on the zygomatic arch and two tuberosities on the lower jaw. Their functions are uncertain; perhaps they were for muscle attachments. The neck was short; there were high spines in the anterior thoracic region for the support of the heavy head, giving the back a humped appearance. Radius and ulna were fused; and, although no cannon bone was formed, the lateral toes were reduced to vestiges. These large beasts were not closely related to the true swine but resembled them in many features and may have been similar in habits.

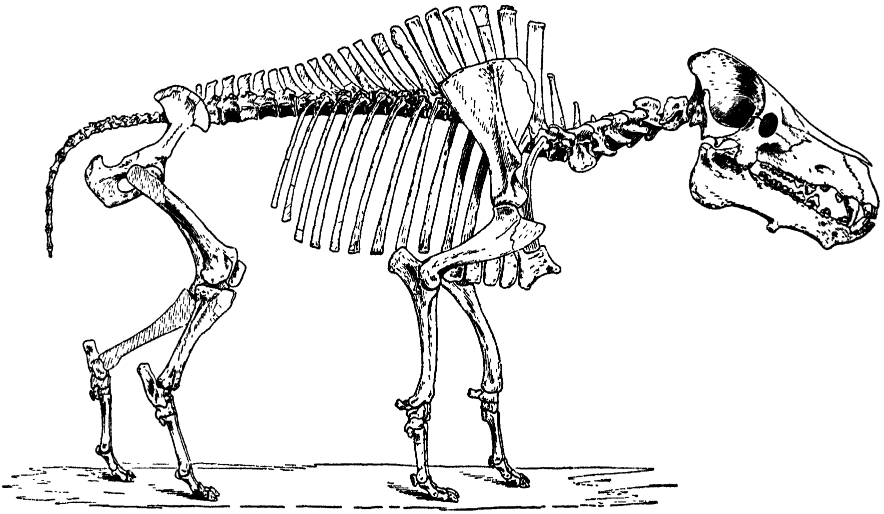


FIG. 339.—*Dinohyus*, a giant piglike artiodactyl (Entelodontidae) from the Lower Miocene of America; original about 10½ feet long. (From Peterson.)

Pigs and peccaries.—The most widespread of Suina in late Tertiary times and, except for the hippopotamus, the only survivors of the group are the pigs and peccaries. In these forms the skull (Fig. 338, *E*, *F*), low in front, ascends steeply toward the back of the head. The orbits are open behind. The canines have a persistent growth and are especially powerful in the males. The dentition (Fig. 336, *D*) is often complete, but an incisor or the first premolar may drop out. The lateral toes, although usually complete, are small and function only on soft ground.

The typical pigs are Old World forms and have never penetrated America. A characteristic pig feature is that the upper canines curve outward and upward, a peculiarity which reaches its extreme in the babirussa of the East Indies, in which these teeth coil upward in hornlike fashion over the forehead. Besides the typical wild boar and the domesticated varieties (*Sus*), various specialized types are present in the Old World tropics. There were numerous genera of fossil pigs in the Pliocene, Miocene, and Oligocene of Eurasia. True pigs are unknown in the Eocene, but some of the rather poorly known Suina of that period may be reasonably regarded as swine ancestors.

The living peccaries of the New World (*Dicotyles*) are obviously related to the pigs but have had a long separate history. A key character is found in the fact that the upper canines have remained in the normal vertical position. The molars (Fig. 337, *E*) are comparatively short and are simple in appearance in contrast with the wrinkled teeth of the Old World hogs (Fig. 337, *F*). In some peccaries the side toes are much reduced (Fig. 342, *B*). There is the beginning of the formation of a cannon bone, and radius and ulna become fused. In these features the peccaries are much more progressive than their Old World relatives.

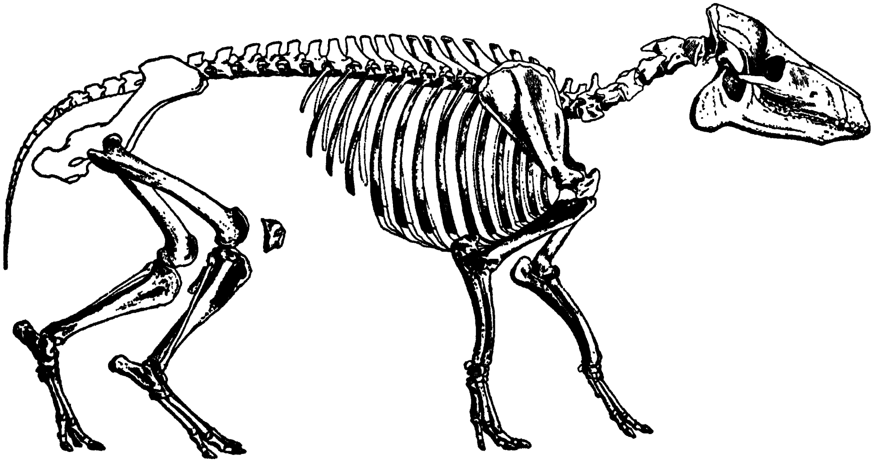


FIG. 340.—*Bothriodon*, an Oligocene anthracothere, about 5 feet in length. (From Scott.)

The modern peccary ranges through South America, which continent it presumably reached only in the Pleistocene, and as far north as Texas. In the Pleistocene, *Platygonus* (Fig. 341) and several other forms were widespread in temperate North America. The oldest-known American peccary is *Perchoerus* [*Thinohyus*] (Fig. 338, *F*), of the Oligocene. It seems certain that the peccaries are an offshoot of the primitive pigs, and certain Oligocene and

Miocene Eurasian genera appear to represent persistent Old World peccaries.

Anthracotheres.—*Anthracotherium* and *Bothriodon* (Figs. 342, *A;* 338, *C;* 340) were typical members of a group of rather large but primitive artiodactyls common in the middle Tertiary of the Old World. The general impression is that of a rather piglike form. The limbs were short, with four functional toes and with a persisting pollex in early genera. The skull was low and generally with a long facial region. Except in some Eocene genera, the mastoid exposure had been reduced, as in the Suina generally. The dentition was complete, with incisors and canines normally developed. The molars were low crowned; some early anthracotheres were bunodont, but later forms (exceptional in the present suborder) tend to develop a simple selenodont pattern. In most anthracotheres the five-cusped, upper-molar pattern characteristic of ancestral types persisted. The position of the anthracotheres has been much debated; but, except for the selenodont tendency in the cheek teeth, their affinities seem clearly to lie with the swine group.

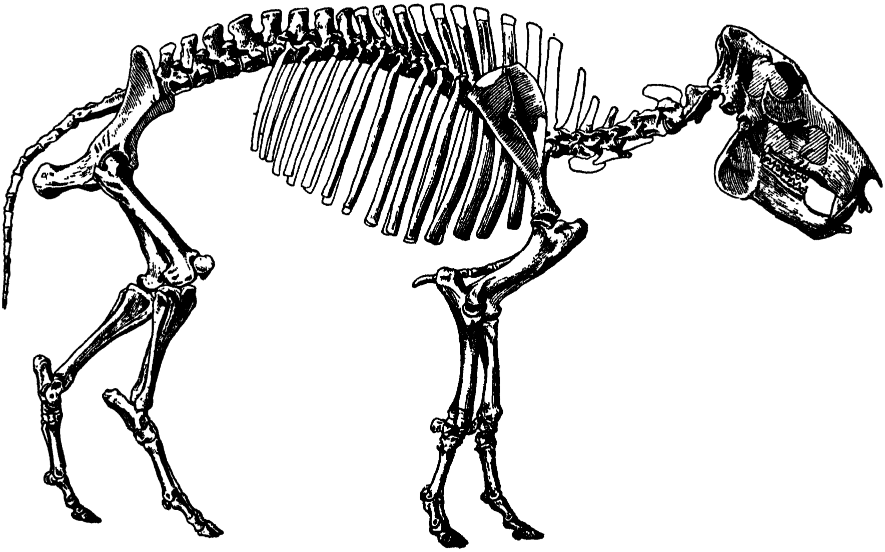


FIG. 341.—*Platygonus*, a Pleistocene peccary, about 3½ feet long. (From Hay.)

The conditions under which anthracothere remains are found strongly suggest that they were amphibious, comparable in habits to the later hippopotami. Numerous remains of early anthracotheres have been found in the Upper Eocene of Asia, and that continent appears to have been the center of development of the group.

Anthracotherium was a long-lived Old World genus. *Bothriodon* [*Ancodus*] was one of several genera which invaded North America in the Oligocene and Miocene; the group made little headway in the Western Hemisphere, however, possibly owing to competition with oreodonts of similar habits. In the Old World, *Merycopotamus* was a late survivor in the Pleistocene of the tropics.

Hippopotami.—The hippopotamus is the only living amphibious artiodactyl. All known forms, living or fossil, may be included in the single genus *Hippopotamus* (Figs. 337, *G;* 338, *D*) and have been confined to the Old World. The hippopotamus lives on soft, water vegetation which is cropped with the heavy anterior teeth and lips. The incisors, flanked by the canines, are set in a transverse row in the broad snout. All the teeth are present in the hippopotamus except the outer incisors, and even these were present in some fossil types. The molars are rather piglike, bunodont with four major

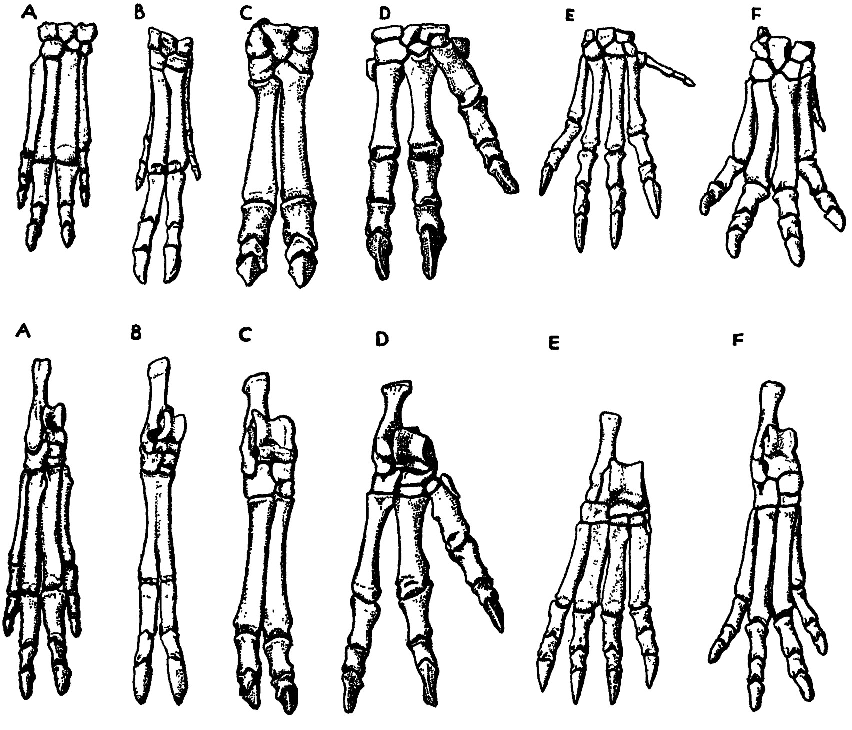


Fig. 342.—Feet of various artiodactyls. Manus above, pes below. *A*, *Bothriodon*, an anthracothere; *B*, *Mylohyus*, an advanced Pleistocene type of peccary, with side toes reduced in front, lost behind, and a cannon bone formed in the pes; *C*, *Dinohyus*, a Lower Miocene entelodont; *D*, *Diplobune*, an aberrant three-toed anoplothere; *E*, *Agriochoerus*, a clawed Oligocene American selenodont. In this and in *F*, *Oreodon*, the pollex is preserved. (*A* after Kowalevsky; *B* after Brown; *C* after Peterson; *D* after Schlosser; *E*, after Wortman; *F* after Osborn.)

cusps. The eyes are small and, in correlation with the amphibious habits, are set high up on the skull; there is the beginning of a postorbital bar. The plump body is supported by short, stout legs; four toes, all functional, are present in the broad foot. Today the hippopotami are confined to Africa, but in the Pleistocene they were widespread in the warmer regions of the Old World. A form similar to the larger African races was abundant in Europe, while pigmy types were present on some of the Mediterranean islands and in Madagascar (a pigmy is found today in Liberia). In the Pliocene, hippopotami were present in the Mediterranean area and India, those from the latter region being the more primitive in the possession of the complete set of incisors. Earlier than this their history is uncertain. There is, however, considerable evidence that they are descendants of the anthracotheres, which they resemble in their mode of life and in some structural features. Most anthracotheres were long snouted, but *Merycopotamus* of the later Tertiary has an expanded muzzle suggesting the initiation of hippopotamus snout specializations; further, while most anthracotheres had five-cusped upper molars, this genus has reduced to a four-cusped type, from which the hippopotamus tooth might have been derived.

Primitive ruminants: the tylopod assemblage.—Much more numerous than the Suina in both fossil and Recent states are the Ruminantia; camels, deer, giraffes, and cattle are but a few conspicuous representatives of a vast array of ruminant types. As the name implies, the cud-chewing habit, associated with the development of a complicated stomach, is a diagnostic feature. Numerous common characters or trends are likewise present in the skeleton. The cheek teeth are invariably selenodont in pattern; the anterior portion of the dental series is much modified, usually with reduction of the canines; the mastoid region remains exposed on the surface of the skull; the limbs are elongated in modern genera, with marked reduction of the lateral toes and with cannon-bone formation.

The living ruminants are divisible into two groups, or infraorders, Tylopoda and Pecora, the first including only the camels and llamas, the second all the remaining forms. Of the two, it is obvious that the Tylopoda are the more primitive, despite specializations seen in living genera. Carpal and tarsal bones, fused to a greater or lesser degree in Pecora, remain distinct. In pecorans the lower canine has become incisiform, so tnat there appear to be four spoon-shaped incisors in each jaw half, and in all living members of the group the upper incisors are lost; the modern camel dentition has been modified to a lesser extent, although there may be reduction and change. If we trace the ancestry of the Pecora back through the Tertiary, we find that they are relatively rare in the Oligocene and almost unknown in the Eocene. The camels, on the other hand, when followed back to the Eocene, are seen to take origin from a varied array of early and primitive ruminant-like artiodactyls which decrease in importance in later Tertiary stages. This complex of primitive ruminants is sometimes included, in whole or in part, under such terms as Bunoselenodontia, Protoselenodontia, or Ancodonta. We shall here include them in the Tylopoda in a broad sense, although recognizing that the modern camels are specialized remnants rather than generalized representatives of this archaic ruminant group.

In Eocene groups included in the Suina we have noted the appearance of genera which tended to preserve a primitive short-limb structure and a primitive disposition of the incisors and canines, coupled with the development of five-cusped upper cheek teeth with a bunodont pattern. Most of the early ruminants here included in the Tylopoda agreed with them in a conservative limb structure and in an upper molar pattern of five cusps in most Eocene genera (later types reduced to four). In other respects, however, they differed sharply from the swinelike forms. The cheek teeth rapidly assumed the selenodont pattern of modern ruminants, and (perhaps with the adoption of a purely herbivorous diet) the anterior part of the tooth row changed markedly. Instead of the generalized condition of sharply accentuated canines separating incisors from premolars, the teeth here tended to become evenly graded without break from incisors past the canines to the adjacent premolars. The lower canines are always reduced and are hard to distinguish from their neighbors. The upper canines are sometimes prominent; but when this condition is found in later camels, it is surely due to secondary growth of the canines; and the same history may be true in other instances.

In this tylopod group of primitive ruminants we include the Caenotheriidae, Anoplotheriidae, Oreodontidae, Agriochoeridae, Camelidae, and Xiphodontidae. These families were prominent in the late Eocene and Oligocene. Beyond that time, however, only the oreodonts and camels of America persisted into the later Tertiary, and of the entire assemblage only the highly specialized camel family has survived.

Caenotheres.—*Caenotherium* and related genera characteristic of the late Eocene and Oligocene of Europe form a family which in most respects shows the primitive tylopod features in diagnostic fashion. *Caenotherium* (Figs. 337, *I;* 343, *D;* 344) was about the size of a hare, and curiously suggestive of hares and rabbits in a number of structural features. This does not, of course, imply any relationship but indicates the possibility that caenotheres (and perhaps the small ancestral ruminants in general) were not unlike the hares in habits and adaptations. Five toes persisted in the manus and four in the pes, but the hind legs were rather elongated, suggesting a bounding (although perhaps not a truly hopping) gait. In the skull the auditory bullae were enormous (as they tend to be in many small mammals), and the antorbital region was fenestrated much as in lagomorphs. The tooth row was an even and continuous one, with the canines indistinguishable from their neighbors. The one nontylopod specialization of the caenotheres is that the protocone has tended, during the evolution of the family, to shift from the front to the back part of the selenodont upper molars.

Anoplotheres.—A second group of archaic Old World tylopods is that of the family Anoplotheriidae. These forms were common in the late Eocene and earliest Oligocene of Europe. Primitive members of the family resembled the caenotheres greatly, but in their five-cusped molars the protocone retained its normal position in the front half of the upper molars. Some of the anoplotheres became highly specialized. *Diplobune*, for example, developed a peculiar three-toed type of foot; *Anoplotherium* (Fig. 343, *B*), common in the late Eocene of Europe, grew to be about 3 feet high at the shoulders and retained bunodont inner molar cusps (Fig. 337, *H*) with a rather peculiar pattern.

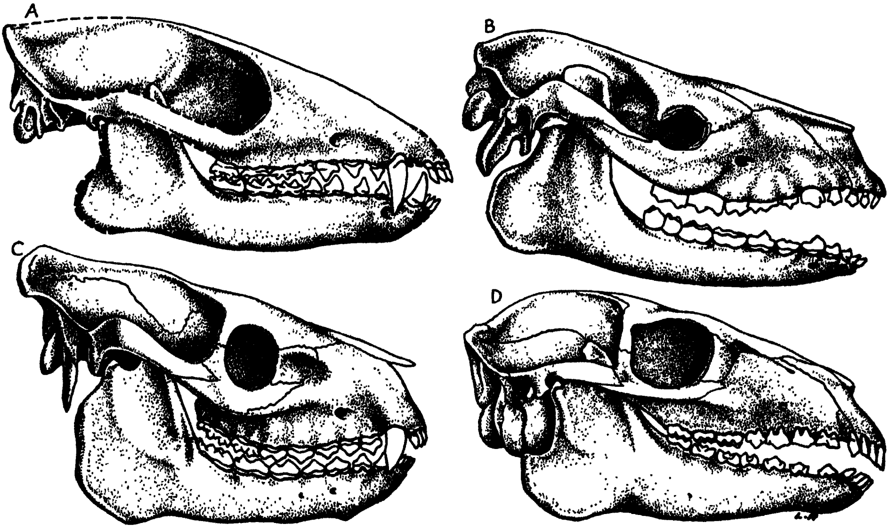


Fig. 343.—Skulls of some early artiodactyls. *A*, *Homacodon*, a primitive Eocene protodont type (jaw restored from a related genus); *B*, *Anoplotherium*, a late Eocene anoplothere, skull length about 14 inches; *C*, *Oreodon culbertsoni*, an Oligocene oreodont, length of skull about 5 inches; *D*, *Caenotherium*, length of skull about 3 inches. (*A* after Sinclair; *B* after De Blainville; *C* after Leidy; *D* after Schlosser and Hürzeler.)

Oreodonts.—The two families just described are unknown in North America. In the late Eocene of this continent, however, there existed, contemporary with the European anoplotheres, a varied series of selenodont artiodactyls in which short limbs, five-cusped upper molars, and a tendency toward an evening-up of the tooth row are features frequently encountered. Some of these genera are thought to be ancestral to camels and to more progressive ruminant groups and will be considered later. At this time, however, there were present still other genera which in most respects exhibit the diagnostic features of the early Tylopoda but were destined to give rise to the most successful of American ungulates of the Middle Tertiary—the oreodonts of the family Oreodontidae (Merycoidodontidae).

Typical oreodonts tended to be rather heavily built animals (Fig. 345), somewhat piglike in general appearance, with short limbs, always four toed and in some cases even with a small pollex (cf. Fig. 342, *E*). The teeth (Fig. 336, *A*), on the other hand, indicate relationship to the ruminants. The tooth row was unbroken, without diastema or loss of teeth; the upper canine was a stout and moderately projecting chisel, but except for this the dentition was comparable to those of the other primitive tylopods just described. The lower canine had been reduced to the size of the incisors and had been functionally replaced by a somewhat enlarged first premolar—a feature which we shall see repeated in some more progressive ruminants. The cheek teeth were strongly selenodont in pattern, usually brachyodont, but rather high crowned in some large and late genera. In typical oreodonts the upper molars are four cusped (Fig. 337, *J*) but in the earliest, Upper Eocene members of the family the five-cusped pattern was still present. The skull was large, the orbit usually closed behind; there was often an antorbital pit or opening presumably containing a facial gland as in higher ruminants.

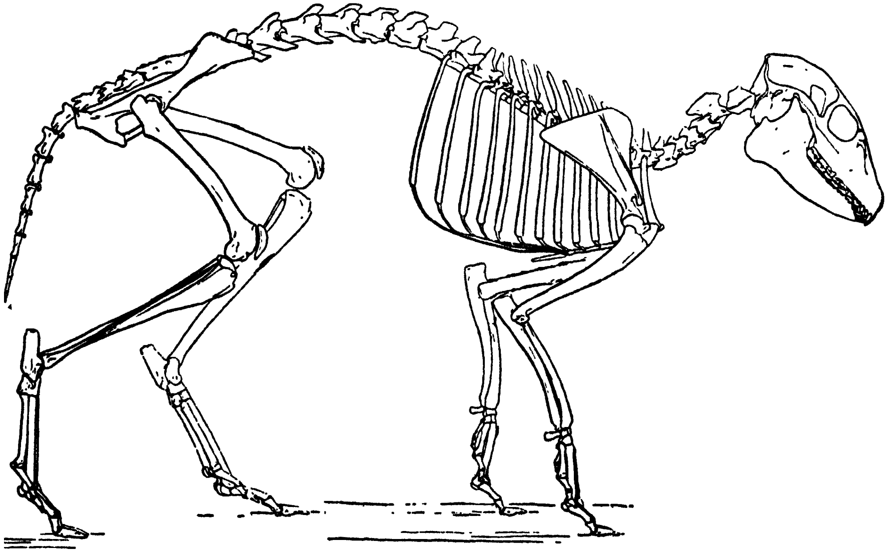


FIG. 344.—The skeleton of *Caenotherium*, a small Oligocene ruminant; length of original about 1 foot. (After Hürzeler.)

This combination of a piglike body build with a more progressive dental structure has led to the popular name of "ruminating swine" for the oreodonts. They seem surely, however, to belong to the ruminant stock and in almost every way to fit into the general group of archaic ruminants with the caenotheres and anoplotheres. But while these European families were rapidly eliminated, the oreodonts of North America flourished for most of the Tertiary, perhaps owing to less intensive competition from higher artiodactyls. There are a few forms from the late Eocene, such as *Protoreodon,* which are more primitive than the later genera in the open orbit and retention of the fifth cusp in the upper molars; had they not given rise to later types they might well have been included in the anoplotheres. In the Oligocene began the expansion of the oreodonts; during the Oligocene and early Miocene, oreodont fossils outnumber all other mammals combined in North American continental strata; the major collecting grounds in the Big Bad Lands of South Dakota, for example, are known as the "Oreodon beds" because of the abundance of the characteristic Oligocene genus *Oreodon* [*Merycoidodon*]. A score of genera were developed. For the most part they remained conservative in structure, but later Miocene genera (such as *Promerycochoerus* [Fig. 345], *Merychyus,* and *Pronomotherium*) and early Pliocene survivors showed specialization in increase in size, development of hypsodont teeth, loss of incisors, and (in the last-named genus) a retreat of the nasal opening, indicating proboscis development.

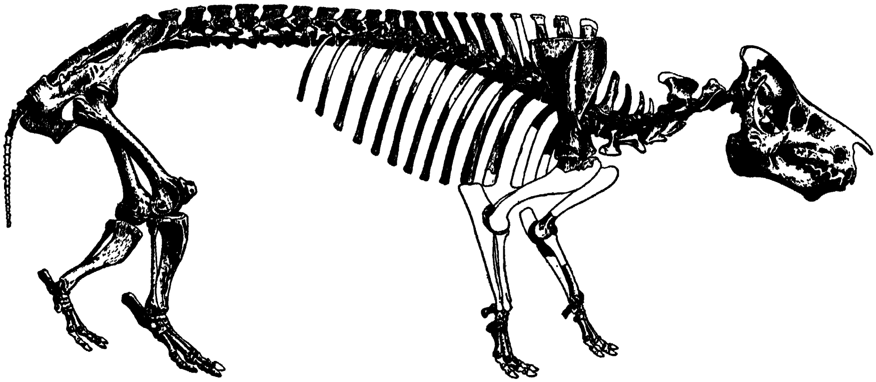


FIG. 345.—*Promerycochoerus,* a Lower Miocene oreodon; original about 5½ feet long. (From Peterson.)

Agriochoeres.—A second American group of primitive tylopods is that of the Agriochoeridae, including *Agriochoerus* and a few other late Eocene and Oligocene genera. In many respects these forms resembled the oreodonts, and, indeed, they are sometimes included in the same family. A striking difference, however, lies in the fact that the feet (Fig. 342, *E*) bore claws instead of hoofs and that the tail was elongated. These forms were persistently primitive in the retention of a pollex. In *Agriochoerus* the upper incisors were lost, and the biting mechanism was presumably similar to that of the higher ruminants. It is difficult to be sure of their mode of life. Perhaps, like the chalicotheres, they ate tubers, while the normal oreodonts may have lived upon soft riverside vegetation, and some of them were probably amphibious.

Camels.—The sole surviving family of the tylopod group is that of the Camelidae, represented today by the Old World camels and the llamas of South America. These are highly specialized forms which, however, can be traced back in the Tertiary of North America to primitive Upper Eocene ancestors, similar in structure to the tylopod families previously considered.

Despite their dissimilarity in superficial appearance, the camel and llama are essentially alike in structure, the hump of the camel and the heavier hairy covering of the South American llamas being probably recently acquired features associated with the habitats of these modern forms. Unlike the majority of the pecora, members of the camel group are never horned. There is a postorbital bar in the living forms; the tympanic bulla is filled with spongy bone.

Modern camelids have a cropping mechanism similar to that of the Pecora, in which the lower incisors extend forward and the herbage is pressed between these and the gums over the premaxillae. The reduction of the upper incisors has taken place at a slower tempo than in the other living ruminants, however; and the lateral one is still retained. A small canine is present, and the premolars have been much reduced with the development of the diastema.

The neck is elongated, and the limbs are long. Ulna and fibula are, of course, much reduced, the latter to a tarsal-like nubbin, and there are no traces of lateral toes. As in the Pecora, the trapezium has gone from the carpus, and the mesocuneiform and ectocuneiform have fused in the tarsus; but the other elements are still separate. The feet (Fig. 348, *B*) are exceedingly characteristic; for, unlike normal ungulates, the living camelids are digitigrade, with spreading toes set nearly flat on the ground, and, instead of a hoof, there is a small nail and a heavy pad beneath the toes.

The division of the stomach into chambers has not proceeded so far in camels as in the Pecora, but the development of stomach pockets for water storage is peculiar to this group.

An early camelid is *Poëbrotherium* (Fig. 346, *A*) of the North American Oligocene, somewhat smaller than a sheep. The dentition was complete, with canines and incisors of similar build and grading over into the elongated premolars with almost no trace of a diastema, as in anoplotheres and caenotheres. The orbit was still open behind, although the two processes which were to bridge the gap were already long. The side toes had already been lost at this early date; the two remaining metapodials were still separate but already showed a tendency toward distal divergence of the two toes so prominent in later camels; the animal presumably had a hoof rather than the modern padded camel foot (Fig. 348, *A*). It is obvious that these camels must have had a separate history well back into the Eocene, for they were at this time more advanced in limb construction than the contemporary Pecora. *Protylopus* and its relatives of the late Eocene appear to represent a still earlier stage in camel ancestry. It is generally agreed that this form is a camelid; but the limbs were short and the front feet four-toed; and, although there are but four upper molar cusps, the protocone has a peculiar forked shape suggesting that it had recently fused with the "extra" protoconule. *Protylopus* is quite similar in most respects to contemporary anoplotheres, caenotheres, and oreodons and indicates the appropriateness of including those types in the Tylopoda, in the broad sense here used.

There were a large number of camelid genera in the later Tertiary, almost all of them until near the end of that period exclusively North American.

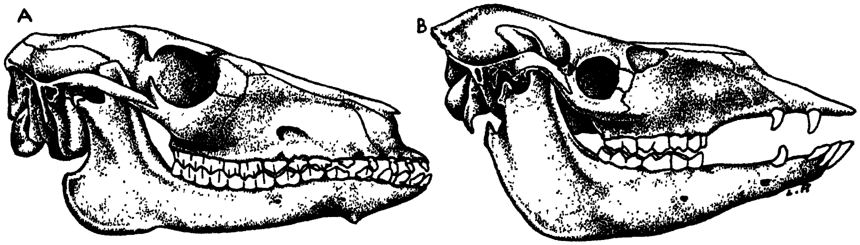


FIG. 346.—The skull of camelids. *A*, *Poëbrotherium*, a primitive Oligocene form, skull length about 6¼ inches; *B*, *Camelops*, a Pleistocene American type, skull length about 22½ inches. (*A* after Wortman; *B* after Merriam.)

Along the main evolutionary line there was a gradual increase in size in Miocene and Pliocene forms such as *Procamelus* and *Pliauchenia*, the orbit became inclosed by bone, a diastema developed, the two inner upper incisors dropped out, and the metapodials fused to form a cannon bone. During the later half of the Tertiary, when camels were numerous in North America, there were many side branches, including such forms as the "gazelle camel," *Stenomylus*, a small and graceful type from the Lower Miocene, and the group of "giraffe camels," such as *Oxydactylus* (Fig. 347), with very long neck and legs.

In the Pliocene appeared forms much closer to the living camelids in which the true ungulate type of hoof was abandoned and the flat, spreading type of toe was developed. The differentiation of modern types was then well under way; at the end of the Tertiary, true camels, *Camelus*, reached the Old World to spread widely there during the Pleistocene, while relatives of the llama, *Auchenia*, reached their present South American home at about the same time. In North America, *Camelops* (Fig. 346, *B*) and other forms not only persisted into the Pleistocene but apparently lived in the Southwest until comparatively recent times. As in the case of the horses, the cause of the extinction of this group in the region which had been so long their home is not obvious, for, when reintroduced during the last century, camels were well able to survive in a wild state in the western deserts.

Xiphodonts.—Often regarded as close relatives of the camels are *Xiphodon* and a few related forms which were very common in Europe on the Eocene-Oligocene boundary. They resembled closely the early camels in both limbs and teeth. They, too, were precociously didactyl, with long, slim limbs retaining only small splints of the side metapodials. As in the ancestral camels, the dentition was complete and without a diastema, and the teeth graded evenly from incisors into the cheek teeth. The upper molars (Fig. 337, *K*) still had the primitive five-cusped pattern, the protoconule remaining distinct. It is probable that the xiphodonts are a European parallel to the camels, developed, like them, from an anoplothere-like stock.

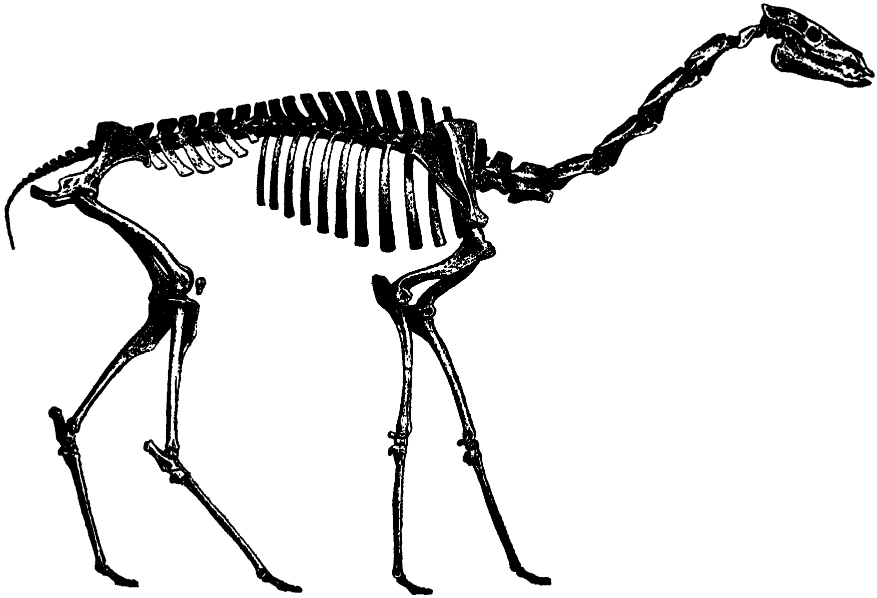


FIG. 347.—*Oxydactylus*, a long-limbed Miocene camel; original about 7½ feet long. (From Peterson.)

The Pecora.—All remaining artiodactyls, including the vast majority of living members of the order, may be included in the Pecora in a broad use of that term. There are five generally recognized modern families and, in addition, several extinct groups. These are here arranged in three superfamilies, one primitive and two advanced, as follows: (1) superfamily Traguloidea, with families Amphimerycidae, Hypertragulidae, Protoceratidae, and Tragulidae (chevrotains); (2) superfamily Cervoidea, with families Palaeomerycidae, Giraffidae (giraffes), and Cervidae (deer); (3) superfamily Bovoidea, with families Antilocapridae (American prongbuck) and Bovidae (cattle, sheep, goats, antelopes).

In these specialized and very successful ungulates the stomach is complicated in structure and the ruminating habit highly developed. The build is, in general, a graceful one; and the limbs are long and slender. All are functionally two-toed types; but reduction of the side digits has gone on at a slower pace than in the tylopods, for small lateral toes are present in a number of living pecorans as well as in many fossil forms. The two principal metapodials have usually fused into an elongated cannon bone. There has been considerable fusion in carpal and tarsal elements, and the union of navicular and cuboid in the ankle is a feature diagnostic of the group. The ulna is reduced, and of the fibula there remains in typical living forms only a nubbin of bone in the ankle region.

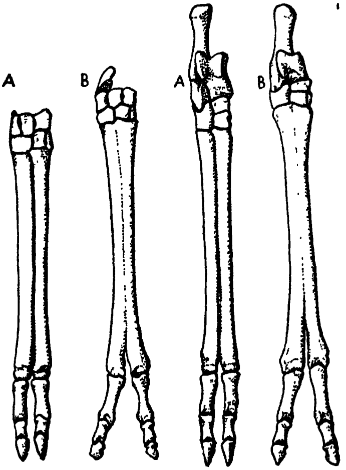


FIG. 348.—Manus (*left*) and pes (*right*) of camels. *A*, the Oligocene *Poëbrotherium; B*, the Pliocene *Procamelus*. (After Wortman.)

Most living pecorans possess weapons in the shape of horns or similar bony outgrowths from the skull. In many primitive types, both living and extinct, these are absent; but long, stabbing upper canines are frequently present in their stead. The upper incisors have given way to a horny pad as part of the cropping mechanism. There appear, at first glance, to be four lower incisors, for the canine has been taken over into the incisor group. One premolar early disappeared with the development of a diastema. The molars have, since early times, been selenodont in pattern with but four cusps—protocone, paracone, metacone and metaconule—in the upper molars.

The chevrotains.—The older pecorans are here included in a superfamily Traguloidea, taking its name from the chevrotains, which alone survive. These forms from the Old World tropics give us some idea of the general nature of ancestral pecorans. Only two genera are present, *Tragulus* of the oriental region and *Hyemoschus* of tropical Africa. Both are small animals about a foot in height and weighing but half-a-dozen pounds. In their small size, retiring habits, and even, at first glance, their general appearance, one would tend to mistake them for rather large rodents, such as the agoutis of South America. But in every structural feature they are good pecorans, comparable to deer or antelope, although with a number of more primitive characters.

The chevrotains are cud-chewers, but the associated subdivisions of the stomach are less complex than in other living pecoran families. Unlike most progressive pecorans, they have no horns or antlers; instead there are (especially in the males) large upper canines as weapons. The upper incisors are absent, as in pecorans generally, and the typical pecoran cropping structure of lower canines and incisors is well developed. The limbs are long and functionally two-toed structures, much more progressive than in any forms considered earlier except the later camels and the xiphodonts; in the tarsus, the navicular, cuboid, and ectocuneiform bones are fused into a unit, a feature known only in pecorans. On the other hand, the limbs are less specialized than in advanced pecoran types. The fibula, reduced in higher families, is still a complete bone, although fused to the tibia. Each foot is four-toed, and the lateral toes, although short and slender, are complete structures, as to both phalanges and metacarpals, whereas the metacarpals are never complete in higher pecorans and the toes themselves are often reduced. In all higher pecorans the middle metapodials are fused in both front and hind legs into a cannon bone. In the living chevrotains such fusion has taken place in the hind limb in both genera; but in the African genus the two metacarpals are still separate, and they are but partially fused in the Asiatic form. In advanced pecorans the keels on the distal ends of the metapodials are present all the way from the dorsal to the ventral surface of the bone; in chevrotains and their fossil relatives the keels are present only on the ventral surfaces, suggesting a different and more limited movement of the toes (Fig. 350, *A*). The front feet are noticeably shorter than the hind, whereas there is little difference in length in higher pecorans.

In various skeletal features, then, the chevrotains are demonstrably on a lower plane of organization than typical pecorans. Absence of horns, large upper canines in the males, limbs relatively unprogressive, particularly the anterior ones, complete side toes, and cannon bones in process of formation—these are characters which we may expect in ancestral fossil pecorans.

Early traguloids.—Primitive pecorans are not uncommon in the Oligocene; in the Eocene, however, they are rare, and the origins of the group are still obscure. Among the oldest and certainly the most primitive of pecoran types are *Amphimeryx* and a few related and obscure genera, known from fragmentary remains, some of which date back to the Middle Eocene in Europe. As far as can be seen from the material, the pecoran characters of the limbs and teeth were, for the most part, already developed. The upper molars, however, show a five-cusped selenodont pattern exactly comparable to that of early tylopods. It is possible that the ancestral pecorans passed through a tylopod stage in their evolution; on the other hand, they may have arisen directly from palaeodont ancestors.

In the late Eocene there are fairly numerous remains of primitive traguloids which had already lost the extra molar cusp but which exhibit in other respects a condition as primitive as that seen in the living traguloids and appear to be very close to the actual ancestry of the existing pecora. *Archaeomeryx* (Figs. 336, *C;* 349) of Mongolia is such a genus; many of the features seen are still preserved in Oligocene types such as *Leptomeryx*. *Archaeomeryx* was about the size of the existing chevrotains and, except for a long tail—presumably primitive—had much of the proportions and probably much of the appearance of these modern genera. In the skull the upper canines were modestly developed. The front limbs were considerably shorter than the hind; the lateral toes and their metapodials were complete. In one item, *Archaeomeryx* has gone beyond the living traguloids, for its fibula had already become reduced by loss of its shaft. On the other hand, it was more primitive than the living genera in two respects: the metapodials were still separate in both front and hind limbs and—most unusually—a full set of incisors was still present in the premaxilla.

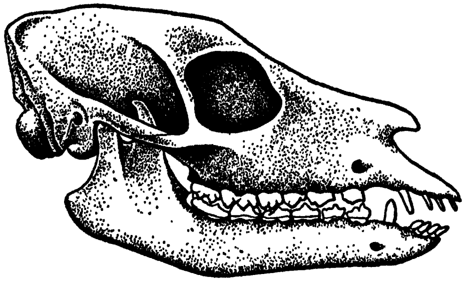


FIG. 349.—The skull of *Archaeomeryx*, a primitive pecoran from the Eocene of Mongolia. (After Colbert.)

Hypertragulids.—*Archaeomeryx*, as we have just seen, is in most respects a primitive pecoran which may lie close to the stem of the suborder. In one feature, however, it shows a specialization not expected in an ancestor of the higher Pecora. Here, as in the oreodons, an enlarged lower premolar has taken the functional place of the canine. This does not occur in the true tragulids or their descendants but is a diagnostic character of the family Hypertragulidae, a group characteristic of the late Eocene, Oligocene, and early Miocene of North America. These American forms have lost the upper incisors, except for occasional vestiges; but in many genera, such as *Leptomeryx* (Figs. 350, *A;* 351; 352, *A*) and *Hypertragulus*, the general structure seen in *Archaeomeryx* has been retained. There are variations, however. The upper canine and the associated lower premolar vary in size—partly, perhaps, as a sexual feature. The lateral metatarsals may be reduced and the medial ones form a cannon, as in *Leptomeryx*. No hypertragulids were of any great size, and *Hypisodus* was a tiny creature no larger than a cottontail.

The Protoceras group.—A series of odd forms, developed in North

America from the hypertragulids, is that best known from *Protoceras* of the Oligocene. In this genus the postcranial skeleton and many skull characters, including the characteristic canine-like lower premolar, are very similar to the hypertragulids. Advances, however, have taken place in other features, such as a considerable elongation of the face and a down-turning of face on braincase like that seen in some of the higher pecorans. Most characteristic, however, is the development in the males of hornlike structures, peaks of bone rising upward in the nasal region, above the orbits and above the braincase roof. Descendants of *Protoceras* persisted into the Pliocene, where *Synthetoceras* (Fig. 352, *B*) shows a grotesque elaboration of two of these horn pairs, the nasal pair forming a curious compound structure.

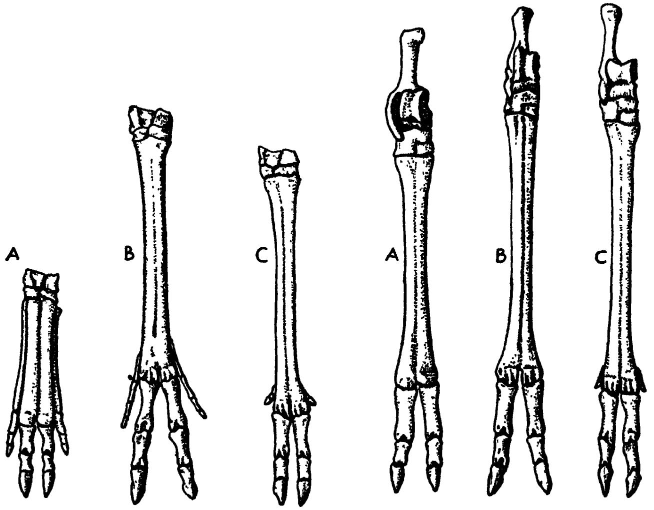


FIG. 350.—Manus (*left*) and pes (*right*) in various Pecora. *A*, the primitive Oligocene *Leptomeryx*; *B*, the Miocene palaeomerycid *Parablastomeryx*; *C*, the Miocene antilocaprid *Merycodus*. (*B* after Scott; *C* after Matthew.)

Tragulids.—Presumably much more important for the evolutionary story than the hypertragulids and their protoceratid descendants were the true tragulids, an Old World stock from which the higher pecorans appear to have descended. In this group absence of the canine-like premolar is a diagnostic character; in other respects the early members of the family appear to be almost indistinguishable from the contemporary hypertragulids. As in that group, the late Eocene and Oligocene genera are numerous and varied. *Gelocus* and *Prodremotherium* are characteristic genera; the former, despite its appearance in late Eocene time, already shows marked reduction of lateral digits in front feet as well as in hind feet. In the Miocene the tragulids were much reduced in numbers, and there remain in the later Tertiary but a few forms, such as *Dorcatherium*, leading to the relatively conservative modern chevrotains.

Higher pecorans.—The remaining pecoran families show progressive features not present in the traguloids. The characteristically exaggerated upper canines of traguloids persist in some primitive forms, but they are typically reduced or absent, and in their stead horns or antlers of some type are usually present as weapons. The progressive development of elongate, two-toed limbs has continued. The ulna is much reduced, except for its head, and is fused to the radius; the fibula has gone, except for a distal nodule—a malleolar bone which looks like an accessory tarsal. Front and hind feet are subequal in length. A cannon bone is universally present and the lateral toes much reduced; never are there complete metapodials, and even the tiny phalanges are likely to be reduced. The keels on the distal ends of the cannon bones are found on the dorsal, as well as the ventral, surfaces. In living forms the presence of four chambers in the stomach offers a contrast to the three-chambered stomach of the chevrotains.

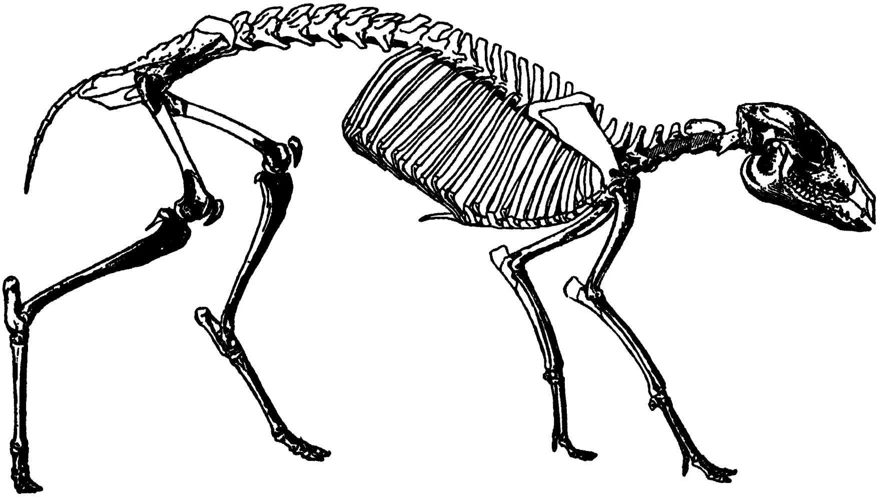


FIG. 351.—*Leptomeryx*, a primitive Oligocene pecoran about 2 feet in length. (From Scott.)

These high ruminants appear in the Miocene. Even at the beginning of their history, however, they show a distinct cleavage into two groups, which we shall consider as the superfamilies Cervoidea and Bovoidea. The former include a basal stock, the Palaeomerycidae, and giraffe and deer families which are derived from them; the latter include the American prongbucks and the bovid assemblage. The cervoids are browsing types, with low-crowned teeth, dwellers in forest or brush country; the bovoids are grassland grazers with high-crowned teeth suitable for siliceous food. As has been

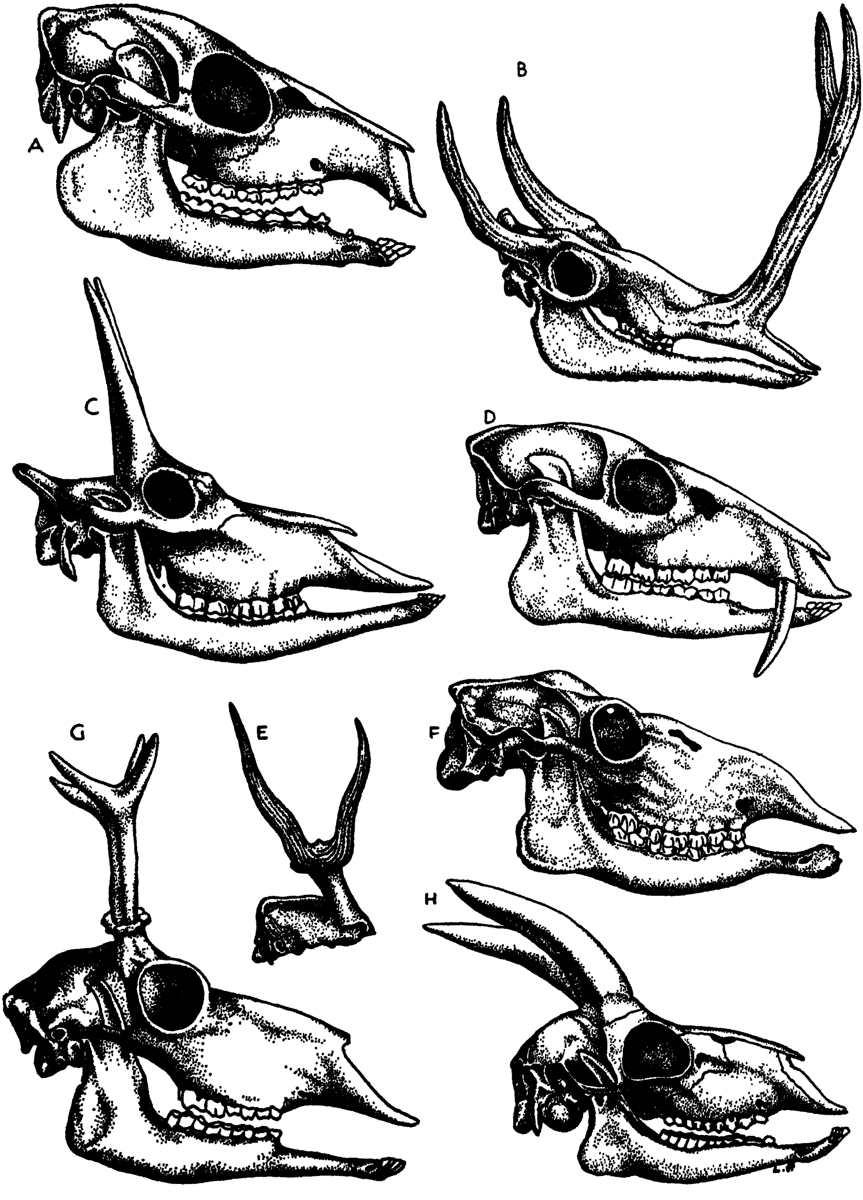


Fig. 352.—Skulls of pecorans. *A*, *Leptomeryx*, a primitive American Oligocene hypertragulid, skull length about 4½ inches; *B*, *Synthetoceras*, a grotesque American Pliocene protocerotid, skull length about 18 inches; *C*, *Samotherium*, a Pliocene giraffe (a male; the "horns" shorter in the female), skull length about 2 feet; *D*, *Parablastomeryx*, a Miocene hornless palaeomerycid, skull length about 14 inches; *E*, horns of *Dicrocerus*, a European late Miocene cervid; *F*, female of *Megaceros*, the "Irish elk," skull length 20 inches; *G*, *Merycodus*, a Miocene antilocaprid, skull length about 7 inches; *H*, *Gazella brevicornis*, a Pliocene antelope, skull length about 6 inches. (*A*, *D*, *G* after Matthew; *B* after Stirton; *C* after Bohlin; *E*, *H* after Gaudry; *F* after Owen.)

said, most have "horns" of some type or other. In the bovoids true horns—bony cores covered by horn (keratin)—are present; in the cervoids these outgrowths lack a horny covering and may be skin-covered, as in giraffes or in growing antlers, or may be bare, as in the mature antlers of the deer.

Palaeomerycids.—In the Miocene of both Eurasia and North America are found numerous pecorans which show many of the features to be expected in ancestors of the deer and giraffes but are not properly assignable to either family and appear to represent a common ancestral stock; these constitute the family Palaeomerycidae. The limbs have the progressive features noted for both cervoids and bovoids; the teeth, as in later giraffes and deer, are low crowned and adapted for a browsing life. A number of these forms, such as the European *Dremotherium* and *Parablastomeryx* (Figs. 350, *B;* 352, *D;* 354) of North America, are innocent of horns of any type and have instead (as have traguloids) stout upper canine tusks. (It must be noted, however, that in cervoids "horns" are frequently confined to the males, and hornless specimens sometimes prove to be females of horned types.) In other genera, however, hornlike structures were present. In a number of types, as *Dromomeryx* and other American forms (Fig. 353), these "horns" were straight bars of bone extending upward at various angles over the orbits. These structures were not, it seems, ever shed, nor is there any evidence of a horny covering. They appear to correspond to the skin-covered bony outgrowths on the skull of a modern giraffe or to the pedicels (usually short) at the base of a deer antler. There are, however, variations in structure; *Cranio-*

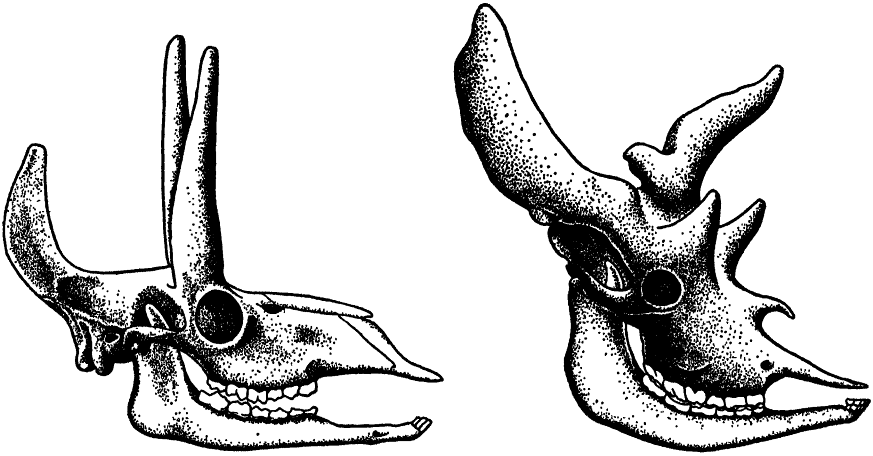


FIG. 353.—*Left, Cranioceras,* a Pliocene palaeomerycid with a median occipital "horn" as well as paired structures; skull length about 1 foot. (After Frick.) *Right, Sivatherium,* a Pleistocene giraffid with large branched horns; size $\frac{1}{10}$ that of original. (After Colbert.)

ceros in North America, for example, had developed a third median horn extending back over the occiput. In *Palaeomeryx* of Europe and in several other genera, short branching structures are found at the tip of the "horn." These are suggestive of simple deer antlers, but there is here no indication that even these terminal outgrowths were deciduous.

Presumably the palaeomerycids gave rise during the Miocene to the Giraffidae and the Cervidae; a few genera persisted into the Pliocene. The group is generally believed to be extinct. A possible survivor, however, is *Moschus*, the "musk deer" of Pliocene to Recent times in central Asia. *Moschus* is usually included among the cervids. It lacks antlers and has large canines, as had palaeomerycids. This in itself does not prove the point, for at least one small true deer is hornless. Various other anatomical features, however, are in contrast with those found in true deer, and it is possible that the "musk deer" is really a palaeomerycid.

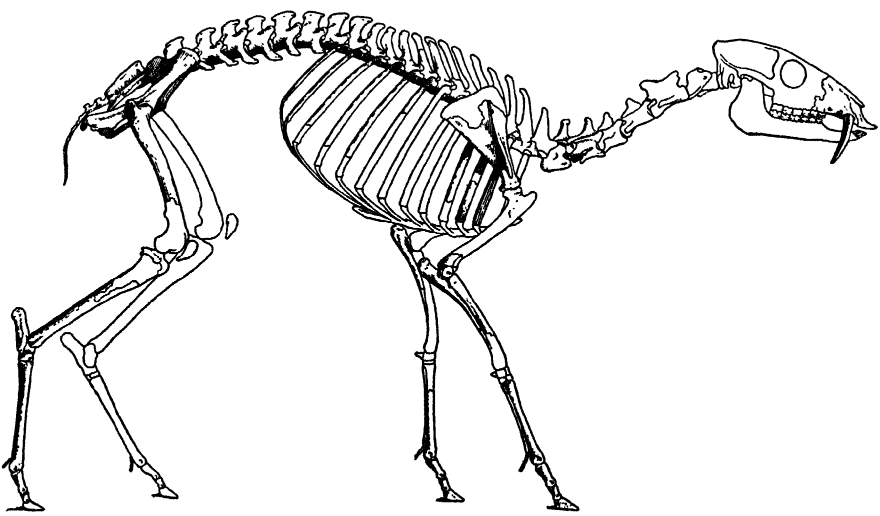


FIG. 354.—*Parablastomeryx*, a Miocene palaeomerycid; original about 2½ feet long. (From Matthew.)

Deer.—The Cervidae are a group of browsers primarily inhabiting the forests of the north temperate zone, in contrast to the more tropical environment favored by the related giraffe group. The most striking feature is the presence of antlers in the males of almost all forms—branching structures of solid bone which project from the skull posterior to the orbits. There is no horny covering; during growth they are surrounded by skin covered with downy hair, the velvet, which dries up and is rubbed off when the antler reaches full growth. Yearly the antler is shed (the place of resorption of bone at its base is marked by a roughened burr) and a new and usually more complex antler developed. This type of structure is in marked contrast to the hollow, horn-covered, unbranched, and permanent true horn of the bovids. The antler is reasonably considered as a further development of the "horns" of the palaeomerycids. These permanent spikes of bone are represented by the much shortened unshed pedicels forming the base of the deer antler; the shed portion—the true antler—is a new cervid addition.

Early small cervids, such as *Stephanocemas* and *Dicrocerus* (Figs. 337, *N;* 352, *E*), appeared in the Miocene and early Pliocene of Eurasia, a region in which the deer seem to have had their origin; and by the end of the Pliocene there were present numerous types, many of which have survived to modern times. Relatively primitive and small deer, little modified from the *Dicrocerus* type, are the muntjacs, *Muntiacus* [*Cervulus*] of southeastern Asia (Pliocene to Recent) and the related *Elaphodus* of India, with very small and simple antlers and persistently large canines. Antlers tend to be more prominently developed in forms of large size, and deer with larger complex antlers are known from the Middle Pliocene onward.

The late Cenozoic and living deer types were formerly all included in the single genus *Cervus*, broadly defined, but are now commonly regarded as constituting a score or more of related genera. The name *Cervus* is generally confined to the European red deer, the American wapiti ("elk"), and a few related types; *Alces* includes the European true elk and the American moose; *Rangifer* the reindeer and caribou (notable for the presence of antlers in the females). The fallow deer (*Dama*) and roe (*Capreolus*) are examples of a number of purely Eurasian types. Except for its northern fringes, Africa has not been invaded by the cervids, but in the Pleistocene the family sent numerous migrants to America. In addition to the forms common to both hemispheres, North America boasted a giant moose, *Cervalces*, in the Pleistocene; and *Odocoileus*, the "Virginia deer," is a purely American development. Pleistocene deer of this last type reached South America and still flourish there in the form of several derived genera. As in many other animal groups, the Pleistocene tended to be a time of production of giant forms; North America, we have noted, developed a giant moose, and in the Old World the "Irish elk," *Megaceros* (Figs. 352, *F;* 355) had the largest antlers of any known deer.

Giraffes.—The Giraffidae today include only the giraffe and okapi of Africa. These are browsing types, with low-crowned but heavy and rugose cheek teeth. Skin-covered "horns" of simple structure, comparable to those of the ancestral palaeomerycids, are present in the living genera and in a number of fossil types. The lateral digits have completely disappeared. The long neck and legs are the most obvious specialization of the modern giraffe and are clearly associated with the tree-browsing habits of the animal. *Samotherium* (Figs. 337, *M;* 352, *C*), *Palaeotragus*, and other forms with a more normal build have long been known from the early Pliocene of southern

Europe and Asia. It was hence of great interest when, about forty years ago, there was discovered in the forests of the Congo the okapi, a comparatively short-legged, short-necked giraffid, almost indistinguishable from such ancestral Tertiary types.

As a side branch of the family may be included *Sivatherium* (Fig. 353) and other forms likewise from the Pleistocene of southern Eurasia and Africa. These were gigantic, heavily built ungulates in which there developed in the males a variety of large "horns," frequently in two pairs, from frontals and parietals. The hinder pair was sometimes massively branched in deerlike fashion but appears to have been nondeciduous in nature.

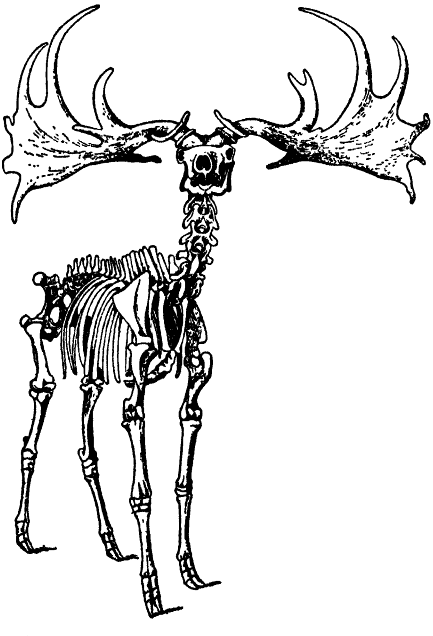


FIG. 355.—*Megaceros*, a giant deer ("Irish elk") from the Pleistocene of Europe. About $\frac{1}{38}$ natural size. (From Reynolds.)

The giraffes are a tropical parallel to the cervid family. They have, however, failed to attain the success reached by their northern relatives.

Bovoids.—The cervoids are browsers; the Bovoidea, the superfamily now to be considered, are the characteristic grazers among the higher pecorans. In them we find the same advanced limb characters as in the cervoids; bovoids, however, tend to be even more progressive than deer in the reduction of lateral digits, for nothing remains of the toe skeleton except nodules of bone in some cases, and even the hoof vestiges may disappear. The upper canines are always reduced or absent, and in correlation with the grazing mode of life the cheek teeth are high crowned. Hornlike structures are universally present; but, in contrast to the cervoids, they are usually present in both sexes, although those of the males are usually more highly developed. Further, the term "horn" is properly applicable to the structures found here, for a sheath of horn covers the bony core, which is never shed.

We have in the case of the bovoids no basal stock comparable to the palaeomerycids in the cervoids. Presumably the bovoids sprang from a traguloid stem and probably from Old World members of the group. There are, however, no connecting forms; both surviving families appear fully developed in the Miocene—the Antilocapridae in North America, the Bovidae in the Old World.

Prongbucks.—*Antilocapra*, the prongbuck of the western plains, usually, but erroneously, called an "antelope," is an isolated and interesting type. While in many features, such as the high-crowned cheek teeth and complete loss of side toes, this form is quite similar to the antelopes, the horns are radically different in character. These structures are, it is true, covered with horn, as in bovids; and the simple bony core is never shed. But the horn is somewhat forked, much as in primitive deer; and, curiously, the horny covering is shed yearly. This suggests that the prongbuck has been long separated from the bovid stock, and it would seem that the living form is a survivor of a North American evolutionary series parallel to the bovids of the Old World.

An early ancestor appears to be *Merycodus* (Figs. 350, *C;* 352, *G*) of the Upper Miocene and Pliocene. This form at first sight would appear to be a deer rather than a prongbuck, for the bony outgrowths from the skull were long, forked (sometimes with several tines), and have a burrlike outgrowth at the base. But these structures were present and complete in all known specimens; it thus seems obvious that, in contrast with the deer, there were horns in both sexes and that these were never shed. The burr may be explained as the point at which an annual shedding of the horny covering occurred.

Merycodus is but one of a series of late Tertiary and Pleistocene types of antilocaprids which appear to have been abundantly present in the American plains in the latter part of the Cenozoic, playing there much the same role (although on a more modest scale) enacted by their antelope cousins in the Eastern Hemisphere. As far as known, all the group appears to have been quite uniform in skeletal and dental structures generally, but there is wide variation in horns. It seems certain that the rather simple horn of the modern prongbuck is a degenerate structure, for in all the fossil types the bony horn is more highly developed than in *Antilocapra* and typically strongly bifurcated—so much so that in the Pleistocene *Tetrameryx* we have an essentially four-horned type.

There are no apparent ancestors for the prongbucks in the Oligocene or early Miocene of North America. One may suppose that the antilocaprids were Miocene invaders from Eurasia, derived from a common ancestry with the bovids.

Bovids.—By far the largest group of living artiodactyls is that included in the family Bovidae, where are placed such forms as the cattle, bison, musk ox, sheep, and goats, and that great and varied assemblage of forms termed "antelopes." In all bovids there are present (usually in both sexes) true horns consisting of a simple unbranched core of bone covered with a sheath of horn; no part of this structure is ever shed.

The bovids have been not only the most successful and numerous of artiodactyls but of ungulates in general in late Tertiary and Recent times; and, as this fact might suggest, their development has taken place at a comparatively late date. They have undoubtedly been derived from the tragulids of the Oligocene, but the first representatives of the family appear in the Old World only toward the end of the Miocene, in the shape of *Eotragus* and a few other rare forms. Eurasia appears to have been the major center of dispersal of these bovids, and literally dozens of genera have been described from the Old World Pliocene, these including the ancestors of many living types.

By the Pleistocene most of them had disappeared from Europe; but in this case, as in many others, Africa and southern Asia have been havens of refuge for forms which increasing cold had forced from the north temperate region; Africa alone contains some twenty genera of living antelopes.

But few members of this group have reached the New World. Most bovids are plains dwellers in warm climates; the dispersal of the group seems to have taken place at such a late date that the cold climate heralding the approach of the Pleistocene glaciation may have rendered the passage through Siberia and Alaska difficult. Only the bison, the mountain sheep, the mountain "goat," and musk oxen, all of which seem to be able to withstand rigorous climatic conditions, have successfully invaded North America; and no bovid has ever reached South America, although the bison ranged southward to El Salvador.

A primitive group of antelopes is that which appeared in the late Miocene and Pliocene in such forms as *Tragocerus*, with horns which were directed upward and backward and were straight, or at the most but slightly curved. Probably rather directly descended from them are a number of large types which have very long but nearly straight horns, also directed backward. First present in the Pliocene, there are still a number of African survivors, such as the oryx and addax antelopes, Side branches of the primitive antelope stock, of which the fossil history is almost unknown, include a number of tiny African forms, some no larger than rabbits, such as the duikerboks and klippspringers. In these forms the horns, still small and backwardly directed, are present only in the males.

The gazelles and related antelopes from northern Africa and southern Asia are steppe and desert forms of moderate size and graceful build, with horns slightly curved but still of a simple primitive type. *Gazella* (Fig. 352, *H*) can be traced back to the early Pliocene. Related to the gazelles is the saiga antelope, with a heavier build and peculiar swollen muzzle; now confined to the arid regions of Asia, it penetrated, in the Pleistocene, westward far into Europe, where its presence is indicative of steppe conditions, and eastward to Alaska.

A northern representative of the bovids is the musk ox, *Ovibos*, heavily built, with massive, laterally directed horns (much smaller in the females). The musk ox is now confined to the arctic zone; but in the Pleistocene, musk oxen penetrated as far south as France and Kentucky, and in North America there were also several related genera, now extinct.

Two further lines of bovid evolution have led to the development of familiar types—to the sheep and goats, on the one hand, and to the cattle and bison, on the other. Pointing out the evolutionary road to the sheep and goats are the types often called "goat antelopes," such as the chamois (*Rupicapra*) of Europe and the Rocky Mountain "goat" (*Oreamnos*), with short but sharply curved horns. In the sheep (*Ovis*) and goats (*Capra*) there has been a great development of the horns, which tend to become very large and often spirally coiled in the males (those of the females are much smaller). These forms are upland dwellers (which may account for the fact that their fossil history is little known), inhabitants of the mountain chains from the Mediterranean region eastward through Asia, and have, as we have noted, even penetrated to the Rocky Mountains.

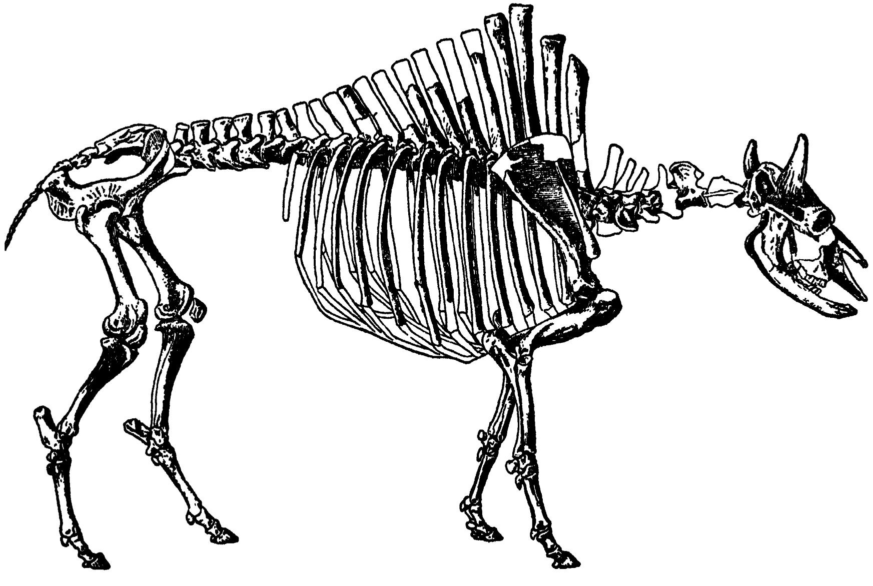


FIG. 356.—***Bison occidentalis***, a Western Pleistocene species, about 7 feet in length. (From Hay.)

The evolution of oxlike bovids appears to have begun well back in Pliocene times with the appearance of large antelopes with teeth rather resembling those of modern cattle and with horns which (although still directed backward) had developed a lyre-shaped form with a spiral twist. Living representatives are the eland of Africa and the nilghai of India. A type still more cowlike and also dating from the early Pliocene is that now represented by the large gnus and hartebeests of Africa, in which the lyrate horns spread sidewise and are, in the former, directed forward rather than backward.

From these cowlike antelopes the development of the cattle has been but a short step. A rather slim and antelope-like ox, *Leptobos*, is found in the early Pleistocene of Eurasia; cattle, most of which may be included in the genus *Bos*, were widespread in the Pleistocene. Common domesticated cattle are but one of several members of this group which have been utilized by man. A large wild ox survived in Europe into medieval times. Closely related to the cattle are the true buffaloes of southern Asia and Africa, now including domesticated types as well as wild forms.

Bison (Fig. 356) is a genus closely related to the true cattle, whose members were dwellers in the temperate regions of the Old World and which, alone of plains-dwelling bovids, has successfully invaded North America. The Old World bison has persisted in a wild state; a few still survive in eastern Europe. In America the bisons became exceedingly numerous in the Pleistocene and seemingly branched out into a number of types, to judge by the variation in fossil horn cores discovered (one specimen had a spread of horns of some 10 feet). Although essentially dwellers in the plains region, Pleistocene bisons were present from the Atlantic to the Pacific.

CHAPTER 24

EDENTATES

GROUPED as edentates in many of the older natural histories is a heterogeneous assemblage of forms from the tropics of both the New and the Old Worlds—the tree sloths, armadillos, and anteaters of South America; the aardvark of Africa; and the scaly pangolins of Africa and southern Asia. In great measure the bonds which were supposed to unite these varied types lay in the nature of the dentition. Some, such as the pangolins and the American anteaters, are toothless; in the others teeth are practically confined to the cheek region and lack the hard enamel covering found in other mammals.

But many of these edentates are ant-eaters, and the reduction or loss of teeth in such types is obviously a functional adaptation and is no argument for their relationship to one another; we have seen that in the aard wolf, an ant-eating marsupial, and the monotreme *Echidna* similar habits have been associated with a similar reduction of the teeth. The aardvark is, it is now generally agreed, quite unrelated to the other edentates. The pangolins, as well, seem to occupy an isolated position; and, aside from specializations for a diet of ants, there is little to connect them with other forms.

True edentates.—As regards the other living "edentates," however, a different situation exists. Comprising, as they do, the South American anteaters, the armadillos, and the tree sloths, as well as the extinct armored glyptodons and giant ground sloths, these New World tropical types exhibit striking superficial differences. But in internal structure there are many features which tend to show that these varied forms really constitute a natural group to which the ordinal name Edentata may be restricted. Xenarthra is an essentially synonymous term.

A striking feature common to all living and most fossil members of the group and not found in any other mammals is the presence of extra (xenarthrous) articulations between the successive arches of the posterior trunk vertebrae in addition to the normal zygapophyses (Fig. 357, *C*). Here, too, are found the only cases (apart from sirenians) in which there is variation from the normal mammalian number of cervical vertebrae; from six to nine may be present. A fusion of the cervical vertebrae may occur.

There are many peculiarities in the limb skeleton of South American edentates. In the shoulder the acromion and the coracoid process are generally much more developed than in other placentals and may join one another (Fig. 357, *A*); the ischium articulates with the proximal caudal vertebrae to form a peculiarly elongated sacrum (Fig. 357, *B*). The limb bones are usually short, stout, and massive, with strong muscular processes. Radius and ulna remain separate, but tibia and fibula have fused in armadillos and ground sloths. Claws are often excessively developed, and in several groups there is a tendency to walk on the outer side of the front foot. Perhaps this is an inheritance from an arboreal ancestor which suspended itself from the branches, as the tree sloths still do today.

The cranial region is characteristic. The brain is small and on a low plane of organization; the braincase is a long, cylindrical tube. The premaxilla is usually reduced, although there is sometimes a supernumerary prenasal bone strengthening the snout. The palate is elongate and may even be bridged over between the pterygoids. Except in armadillos and some glyptodons, the zygomatic arch is incomplete, the jugal often ending posteriorly in a fan-shaped expansion but failing to reach the squamosal.

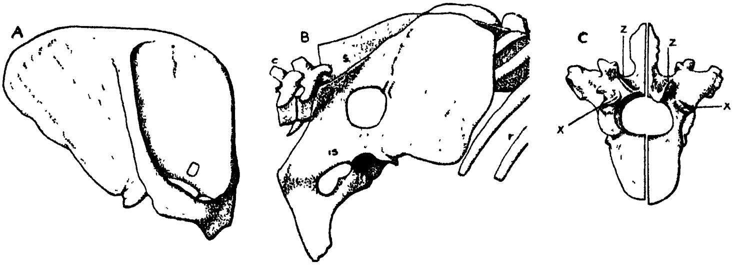


FIG. 357.—*Mylodon*. *A*, Scapula, to show bridge from acromion to coracoid; *B*, pelvic region, showing upward growth of ischium (*is*) to join with sacrum (*s*); *r*, ribs; *c*, caudal vertebrae. *C*, a posterior dorsal vertebra, to show "xenarthral" articulations (*x*) in addition to the normal zygapophyses (*z*). On the left side the anterior view, posterior on the right. (After Stock.)

Only in anteaters have the teeth been altogether lost. In other edentates they are usually absent from the front of the mouth, while roots are never formed in the cheek and there is no enamel covering except in a few early genera.

A tendency toward the development of protective armor in the skin appears to have been inherent in the group. In the armadillos and the extinct glyptodons we find a bony carapace covered by horny scales. No bones are present in the skin of tree sloths and anteaters, but in some of the extinct ground sloths the skin was reinforced by numerous bony nodules lodged in the thick hide.

The center of evolution of these types is unquestionably South America, the present home of practically all members of the group. Ground sloths, glyptodons, and armadillos are known as fossils from the late Cenozoic of the United States; but it is generally agreed that these forms were immigrants from the south. It seems highly probable that the ancestral edentates, like the peculiar ungulates of that region, inhabited South America at the very beginning of the Age of Mammals and there underwent an isolated development during most of the Tertiary.

Palaeanodonts.—If the edentates are assumed to have originated elsewhere and to have reached their southern home by way of North America, it might be expected that some trace of the group would be found in the early Tertiary of the north. This expectation has been fulfilled; three North American genera, ranging from late Paleocene to Oligocene, appear to represent a primitive edentate stock. All three are rare, but *Metacheiromys* (Fig. 358) of the Eocene is known from fairly complete material.

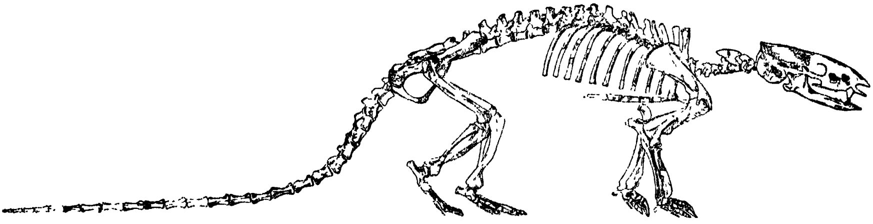


FIG. 358.—*Metacheiromys*, a small Eocene edentate, about 18 inches long. (From Simpson.)

In many ways these forms were much more primitive and generalized than any of the later South American edentates. *Metacheiromys* resembles the armadillos in general proportions and even in many structural details, but there is no trace of dermal armor, and the accessory xenarthral articulations are absent in the backbone. Long, compressed claws were present in the front feet, somewhat shorter and broader ones behind, and even here there was already some tendency for a twist in the wrist.

The teeth show many of the characteristics to be expected in the ancestral edentates, for the incisors had disappeared except for one small lower tooth, the cheek teeth were, at the most, pegs, and nearly all of the enamel covering had been lost. There were, however, some dental specializations not in line with the direct ancestry of South American forms. The canines were large; in *Metacheiromys* the cheek teeth have nearly completely disappeared and may have been functionally replaced by horny pads.

The clawed feet and peculiar dental apparatus of the palaeanodonts suggest that they may have fed upon small terrestrial invertebrates, digging for grubs, insects, and worms much as do modern armadillos.

These North American genera, constituting the suborder Palaeanodonta, appear to represent in most of their features the ancestral edentate type from which the South American forms have sprung. It is obvious, however, that they are too late in time to have been the actual ancestors, for South America was presumably already cut off by the time of their appearance. They were merely wayside stragglers, destined not to survive in competition with the numerous other orders already appearing in North America.

Xenarthrans.—The continuation of the story of edentate development is to be sought in South America. There edentates were already present in the oldest-known Tertiary beds. Although most Eocene remains are fragmentary, it appears probable that the earliest South American representatives possessed many of the features absent in the palaeanodonts but characteristic of later groups, such as the additional vertebral articulations, union of ischium and backbone, and peculiar skull structure.

Among these South American forms there have evolved five distinct types which may be placed in two suborders. One group, the Loricata (armored), comprises the "shelled" forms, the living armadillos and the extinct glyptodons; the other, termed the Pilosa (hairy), includes the anteaters, the tree sloths, and the extinct ground sloths, all hair-covered, unarmored forms.

Loricates.—The great development of dermal armor is the most obvious feature uniting the armadillos and the now extinct glyptodons. A large number of bony plates covered with horny scutes form a protective carapace over the trunk, while plates may develop on the head and tail as well. The teeth tend to be more numerous than in the sloths; there are always as many as seven cheek teeth, often a higher number. The zygomatic arch is usually complete. There is a tendency for a fusion of vertebrae under the shield; and some of the cervicals, at least, are fused in all forms.

In the armadillos, the family Dasypodidae, the carapace never becomes a single solid shield, as in glyptodons. Instead, the bony scutes usually tend to form solid plates over the shoulder and pelvis, between which are transverse movable bands. Beneath the pelvic plates is a long, heavy sacrum, while fused neck vertebrae lie beneath the shoulder plate. The cheek teeth of these insect and carrion feeders are usually simple pegs, about eight to ten in number in each jaw half. There is a tendency to exceed the normal placental number, an extreme being reached in one living form with as many as twenty-five.

These armored types at first sight would seem to be very aberrant. But, curiously enough, they are the oldest-known of South American edentates, for they are the only types represented in the Paleocene and early Eocene beds of that continent. In these beds, there are not merely numerous isolated armadillo scutes but also much skull and skeletal material of the genus *Utaetus*. Furthermore, the structural tendencies seen in palaeanodonts seem to lead more directly to the armadillos than to other edentates. It thus appears probable that the armadillos represent the main stem of the South American edentates, although one dislikes the implication that the "hairy" edentates have descended from armor-bearing ancestors.

By the Miocene, armadillos, such as *Proeutatus* (Figs. 359, *A;* 360, *A*) and *Stegotherium*, were abundant and varied. A peculiar side branch is that of *Peltephilus* and its relatives, which contrast with normal armadillos in their short, broad skulls and the development of hornlike structures in their head armor. With the re-establishment of continental connections, the armadillos pushed north, reaching the Gulf Coast region in Pleistocene times; and one form still persists in southern Texas. In the Pleistocene of both continents there were present giant armadillos, now extinct, one as large as a rhinoceros.

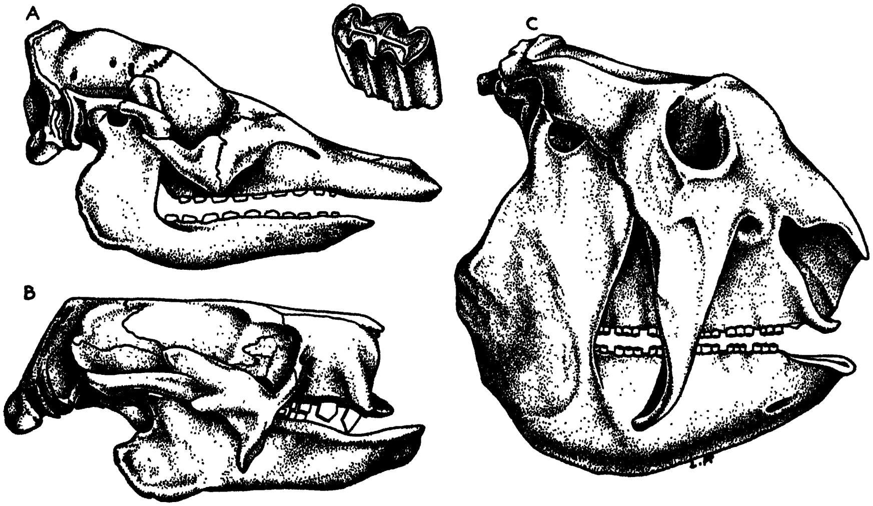


FIG. 359.—Skulls of edentates. *A*, *Proeutatus*, a Miocene armadillo, skull length about 5 inches; *B*, *Mylodon*, a ground sloth, skull length about 20 inches; *C*, *Glyptodon*, skull length about 11 inches. Above, in center, a glyptodont tooth. (*A* after Scott; *B* after Stock; *C* after Burmeister.)

The extinct glyptodons (*Glyptodon* [Figs. 359, *C;* 361], *Panochthus* [Fig. 360, *B*], etc.) were a group related to the armadillos and, like them, had developed a protective armor, but in a different fashion. Originally, it would seem, the bony plates on the back may have been placed in cross-rows, as in the primitive armadillos. But typical glyptodons tended to fuse the entire mass into a solid, turtle-like carapace composed of a mosaic of countless small polygonal plates. There was much fusion of the vertebrae, mainly in connection with support of the shield. Most of the cervicals, except the first, were fused; a second solid mass included most of the dorsals; while the last dorsals, lumbars, and sacrals were fused and connected with the posterior part of the carapace. The tail was sheathed in armor plates, sometimes with projecting spikes. Like the armadillos, these forms were generally five-toed and clawed; but the toes were short and stubby, the claws broad and rather hooflike in the hind feet (the front feet were more variable).

The skull was covered with a bony casque; the face and jaws were excessively deep. In these forms, alone among edentates, there was a postorbital bar, and the zygomatic arch had a long downward-projecting process of the jugal. There was no clavicle, in contrast to most other edentates. The teeth numbered eight in each jaw ramus. They were typically very high crowned and had a peculiar three-lobed pattern analogous to that of some of the ratlike rodents.

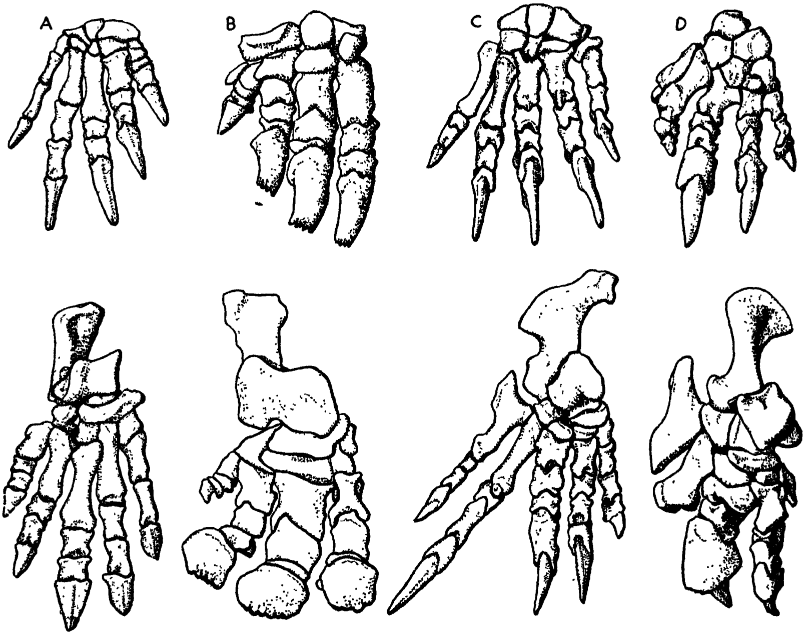


FIG. 360.—Feet of edentates, manus above, pes below. *A*, *Proeutatus*, a Miocene armadillo; *B*, *Panochthus*, a Pleistocene glyptodont; *C*, *Hapalops*, a primitive Miocene ground sloth; *D*, Pleistocene ground sloths, manus of *Mylodon*, pes of *Nothrotherium*. (*A*, *C* after Scott; *B* after Burmeister; *D* after Stock.)

It seems certain that the glyptodons were derived from the primitive armadillos. They appeared at the end of the Eocene and were well represented in the Miocene beds of South America. These earlier forms were small compared to the later members of the group but were already of larger size than most of the contemporary armadillos. There were still present many primitive armadillo-like characters, such as the comparatively long skull, low-crowned teeth, and the persistently primitive arrangement of some anterior plates in more or less transverse rows. By the Pliocene, large size and characteristic glyptodon structure had been attained. These huge armored forms early migrated northward, and one genus had reached Texas at the end of the Pliocene. In the Pleistocene the glyptodons were numerous from Florida to Argentina. Here again, however, as in the case of most large land mammals in the Western Hemisphere, the end of the Pleistocene witnessed the extinction of the group.

Living "hairy" edentates.—The remaining South American edentates may be grouped as the suborder Pilosa, the name referring to the hairy covering of these animals and the absence of a carapace. The zygomatic arch is always incomplete, although the jugal is usually much expanded posteriorly. There are never more than four or five simple cheek teeth. Among the peculiar features in the skeleton may be noted the fact that the expanded acromion arches forward to unite with the coracoid region (Fig. 357, *A*). Included in this group are the anteaters and tree sloths inhabiting the tropical forests of South America and the extinct ground sloths.

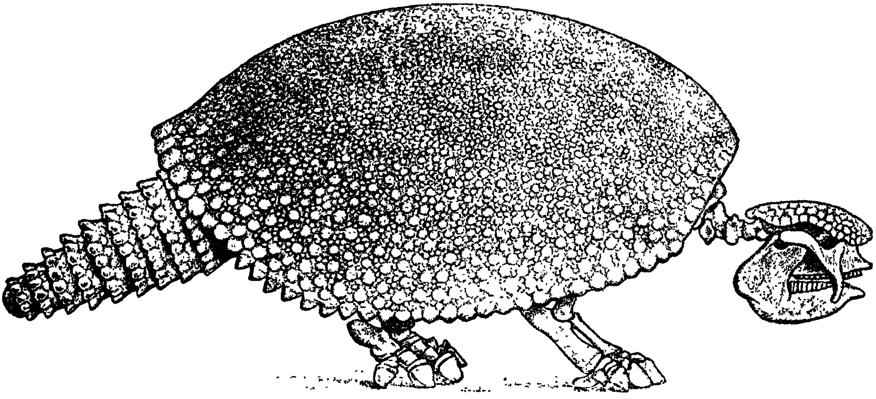


FIG. 361.—*Glyptodon*, from the Pleistocene of South America, length about 9 feet. (From Lydekker.)

The anteaters, *Myrmecophaga* and related forms, exhibit specializations which seem but a logical outcome of the insect-eating habits of the palaeanodonts. In the front feet are developed large claws (particularly on the middle toe), which are used for digging into termite nests; the lateral toes are reduced. With the presence of these large excavating tools it has become impossible for the foot to be placed flat upon the ground, and the weight rests on a pad on the outer side of the knuckles with the toes turned inward. In the hind foot the claws are smaller, and the foot is plantigrade in the more primitive types.

The postcranial skeleton of the anteaters seems to be of the type which would be expected in the ancestors of the remaining groups of edentates. But the highly developed termite-eating habit has been associated with great modification in the head region. There is a very long, tubular snout containing a protrusile, whiplike tongue; the jaw is weak; and these forms, alone among true edentates, have entirely lost their teeth.

The living tree sloths of South America included in the family Bradypodidae are among the most curious of mammals. They are small, arboreal, nocturnal forms with a lichenous growth which often gives a green tinge to their gray hair. They are very slow and clumsy, spending much of their time hanging upside down from branches and holding on by their long curved claws, two or three in number. The front legs are longer than the hind; the body is elongated; but the tail is vestigial. These leaf-eating types have but four or five cylindrical cheek teeth, one of which is anteriorly placed and may be a canine. The skull is very short in the facial region, and there is only a tiny premaxilla. The jugal ends posteriorly in a flaring termination.

The tree sloths are unknown as fossils and the anteaters are known only from fragmentary material from the later Tertiary and Pleistocene. Remains of these forest dwellers are not to be expected in the deposits of the Argentinian plains from which most of the older South American fossils are obtained. But even in default of fossil evidence, it is not impossible to gain some idea of the nature of the primitive stock of the Pilosa from which these two types have been derived. Very probably this ancestral form would have had a rather omnivorous diet (as is still the case in armadillos), with a dentition comprising a small number of peglike cheek teeth in a moderately elongate skull. Presumably the ancestor would have been a long-clawed, terrestrial, grubbing form with much the proportions and foot pose of the terrestrial anteaters. From this type the anteaters have departed mainly in cranial features connected with their food habits, the tree sloths in body changes related to their specialized arboreal life.

The requirements for this hypothetical primitive ancestor are very closely approached in some of the more primitive ground sloths; and these, in turn, are not too far removed in postcranial structures from the armadillo type.

Ground sloths.—The large and numerous forms of the ground-sloth group in the Pleistocene of both North and South America are among the most interesting of extinct mammals. The ground sloths first appear in the Oligocene of South America. Of the three families into which these forms are usually divided, the Megalonychidae are perhaps the most primitive and are the first to assume importance, being common in the Miocene but relatively rare in later times. The characteristic Miocene *Hapalops* was (for a ground sloth) small in size, with a length of but 4 feet or so, including the elongate tail. The body was moderately long and rather slender in its build. A full complement of clawed toes was present (Fig. 360, *C;* cf. 360, *D*). The claws were particularly well developed on the front foot, which was twisted over to rest the weight on the outer knuckles, while the stocky hind foot was turned downward laterally so that the weight rested on its outer margin. The skull was moderately elongated; slim premaxillae above and a spoutlike process from the jaws presumably supported horny cropping plates; in the cheek there were present, as in ground sloths generally, five simple teeth above and four below, the first resembling a canine in this and other megalonychid genera. The zygomatic arch was incomplete; but the huge jugal, which splays out into a number of projections posteriorly, came close to the anterior end of the squamosal.

Nothrotherium (Fig. 362), was a descendant of *Hapalops* found in the Pleistocene of both North and South America. Its size, about that of a tapir, was relatively small for a ground sloth of that age, and there were few further modifications except for the loss of the "canines." It persisted to a very late date in the southwestern United States, for not only has a skeleton been found with much of the skin and tendons still preserved, but it also appears that this form was a contemporary of early man. Other small members of this family have been found in Pleistocene deposits in the West Indies. These forms range in size from cat to bear, the dwarfed condition presumably related to insular life. How they reached those islands is an interesting problem in geographical distribution.

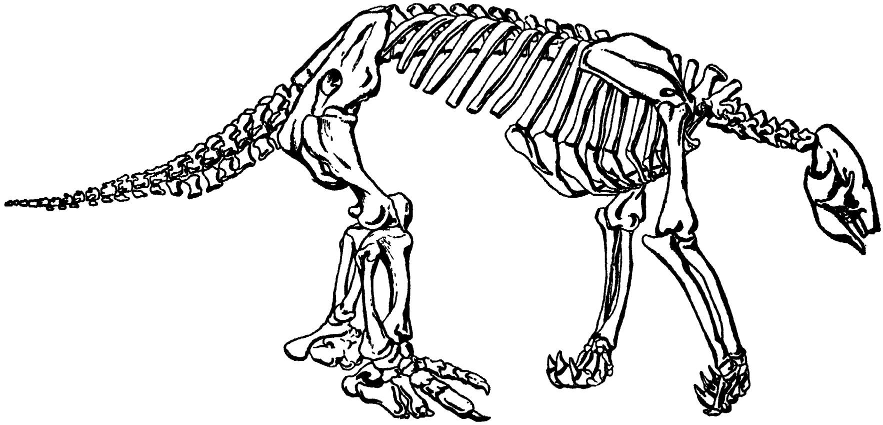


FIG. 362.—The skeleton of *Nothrotherium*, a small Pleistocene ground sloth; length about 7½ feet. From Stock.)

Most of the ground sloths of the Pliocene and Pleistocene tended to grow to very large size. This was accompanied by many structural changes, with the body much more massively built in relation to the requirements for weight support. The one common member of the present family in which large size was attained was *Megalonyx* of the North American Pleistocene, about the size of an ox with a skull a foot in length. It seems to have been nearly a direct descendant of *Hapalops* and, while much more heavily built, resembled that form in many features.

Megatherium **gives its name to a family of sloths which are related to the**

megalonychids and probably derived from them but which differ in certain diagnostic features, such as the lack of specialization of the "canines," reduction of the two inner toes, and cheek teeth which simulate a bilophodont condition. *Megatherium* ranged from South America to the southeastern United States in the Pleistocene. This largest of ground sloths exceeded an elephant in size, with a length of 20 feet and a very massive build.

The Mylodontidae were the most abundant of ground sloths in the Pleistocene, *Mylodon* (Fig. 359, *B*) and its close relatives being found from Patagonia to temperate North America. Large size was common in the late mylodonts; *Mylodon,* for example, was half again as large as the contemporary *Megalonyx.* Diagnostic features include a partial development of "canines," a rather triangular shape in the cheek teeth, and a hind foot in which the first toe (but not the second) had been reduced. In the mylodonts round ossicles deeply imbedded in the skin seem to have afforded a defense against enemies. *Mylodon*, like *Nothrotherium,* appears to have been a late survivor in the southwestern United States; and a closely related type found in a Patagonian cave appears to have been killed by man.

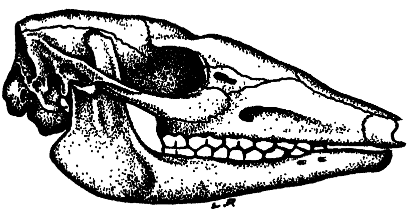


FIG. 363.—*Orycteropus gaudryi,* a fossil aardvark from the Lower Pliocene of Samos; skull length about 6¼ inches. (After Andrews.)

Ground sloths flourished greatly in the Pleistocene. But at the close of that period they were utterly wiped out. Why, we cannot say. Unlike the South American ungulates, which seem to have disappeared when faced by progressive competitors, the ground sloths had not only held their ground but had successfully invaded North America. The factors causing their extinction are as mysterious as those which destroyed most of the other larger mammals of the Western World.

Pangolins.—The Old World "edentates," the pangolins and aardvark, may be considered here for want of a better connection.

The scaly anteaters or pangolins of tropical Asia and Africa, constituting the genus *Manis,* are the sole representatives of the order Pholidota. The horny overlapping scales completely covering the body form the most notable peculiarity of these animals. This covering is probably a secondary protective device and not due to direct inheritance from reptilian ancestors. With the adoption of an ant-eating diet there have developed many cranial adaptations similar to those of American termite-eaters. Teeth are completely absent; there is a long snout, a slim jaw, and a long tongue. The temporal arch is incomplete and the jugal lost; the eyes are much reduced. The tail is usually long, sometimes prehensile. All toes are present; but the hand is functionally tridactyl, with the development of powerful digging claws.

Representatives of the living genus have been found in the Pleistocene of southern Asia. A few bones from the Miocene and Oligocene of Europe have been thought to belong to this group but tell us nothing of their pedigree. Relationship with American edentates has been often suggested, but the similarities are such as are obviously related to digging and to eating ants; there are no positive resemblances to the xenarthrans. The pangolins may have evolved quite independently from some early primitive placental stock.

The aardvark.—Quite isolated, too, is the "earth pig," *Orycteropus*, sole living representative of its own order, the Tubulidentata. This is an uncouth-looking African mammal which lives on termites. There is a long snout, a small mouth, and a long tongue, as in other ant-eating mammalian types; but there is comparatively little reduction of the jaws, and the temporal arch is well developed in contrast to other ant-eaters. In the embryo, teeth are numerous, exceeding the usual placental number; but in the adult only four or five peglike cheek teeth remain. These lack enamel but have cement on the outside; while, instead of a pulp cavity, the dentine is traversed by a large number of small tubules, a feature to which the group owes its name.

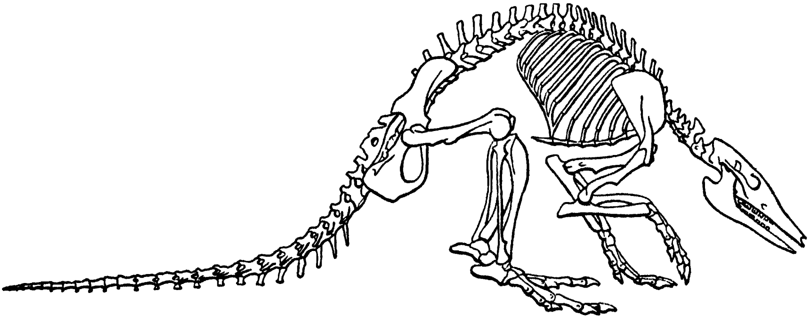


FIG. 364.—The skeleton of *Orycteropus gaudryi*, length about 3½ feet. (After Colbert.)

There are a number of primitive skeletal features. Tibia and fibula, however, are fused proximally, and the pollex has disappeared. The feet are semiplantigrade; and there are stout "nails," intermediate between claws and hoofs in nature, inserted in fissured end-phalanges, much as in some early carnivores.

Fossil aardvarks (Figs. 363, 364) ranged through Eurasia in the Pliocene in company with the ancestors of many other living African types. Back of that there are in Europe but a few doubtful fragments from the Oligocene and Miocene. In the Lower Eocene of North America have been found fragmentary remains of *Tubulodon*, a form which shows a tubular structure of the teeth somewhat similar to that of aardvarks. The aardvark skeleton is strikingly similar to that of some early condylarths, and it is possible that it is descended from early ungulates.

CHAPTER 25

WHALES

AMONG mammals which have turned to an aquatic life, the whales—the order Cetacea—constitute the largest and most important group and that best adapted to an existence in the water. Both structurally and functionally they have become completely divorced from their former land life and are helpless if stranded. Only in their need for air breathing do they exhibit any functional reminiscence of their former terrestrial existence.

Modern whales have reassumed the torpedo-like, streamlined shape of primitive aquatic vertebrates, partly through a shortening of the cervical vertebrae and the consequent absence of a neck. However, the body is thick and rounded in section, and hence (unlike the typically slimmer fish) the main propulsive force is confined to the tail fin alone. As in other aquatic mammals, the tail has failed to resume its original fin structure, and (as in the sirenians) horizontal flukes supported by fibrous tissue supply the locomotive power. A dorsal fin has usually redeveloped. The hind limbs are lost completely, as far as any superficial indication goes, although vestiges may be present internally. The front legs have been transformed into short, broad, steering flippers. Although there are no extra digits, as many as a dozen extra phalanges may be present. Hair has been lost and may be absolutely lacking on the skin of the adult whale; a thick layer of blubber affords protection against cold.

Marine life has been accompanied by many internal modifications. The original whales appear to have been fish-eating carnivores. The majority of modern whales are still toothed, but, as in the seals, the teeth have been simplified, usually into simple pegs. The number has in many cases increased greatly over the primitive placental forty-four; in others teeth have been reduced in number or entirely abandoned for a straining apparatus of whalebone. The anterior portion of the skull has been elongated from the first. But in correlation with the breathing problem in diving types, the nostrils have moved backward in the skull and in typical living whales are placed, as the blowhole, on the top of the head (Fig. 365, *B–D*). In this process the premaxillary and maxillary bones have been dragged back over the more posterior elements, often in an asymmetrical fashion. This results in a peculiar,

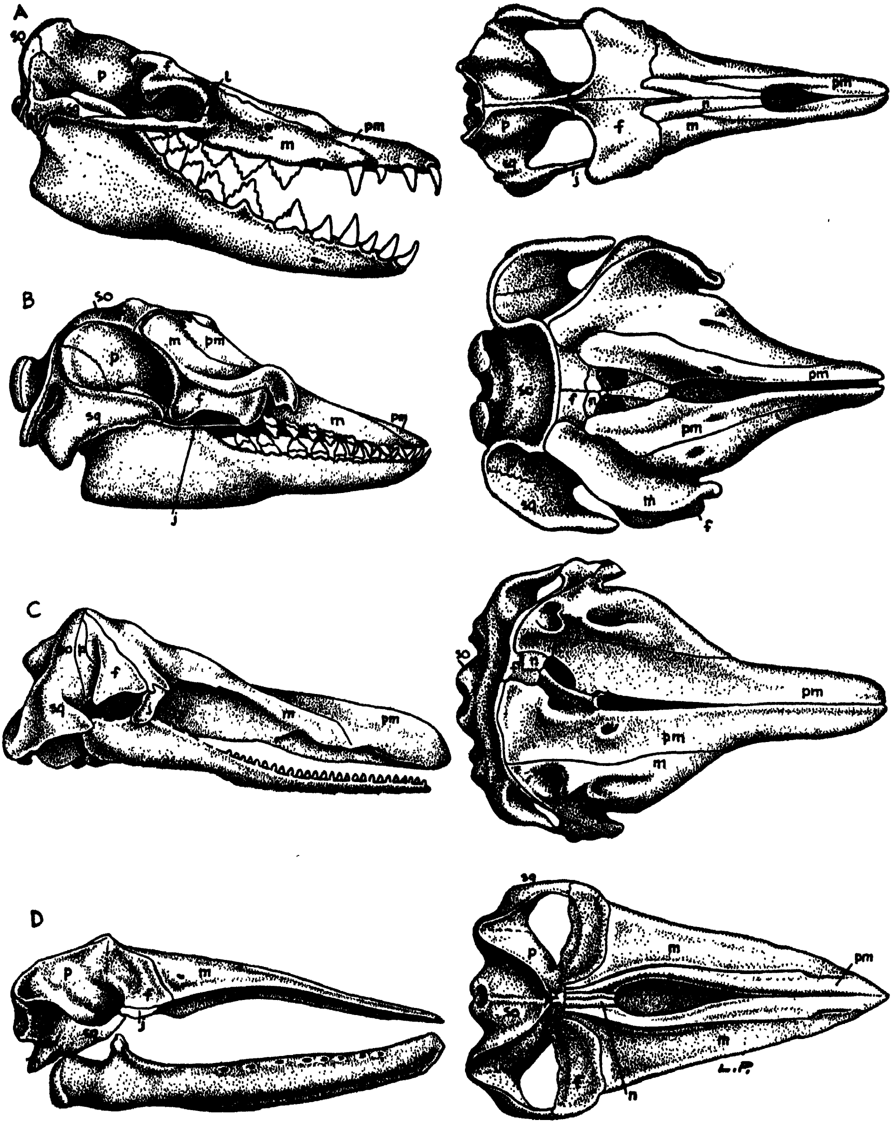


FIG. 365.—Skulls of cetaceans, lateral and dorsal views. *A*, *Prozeuglodon atrox*, an Eocene archaeocete, skull length about 2 feet; *B*, *Prosqualodon*, a Miocene squalodont porpoise, skull length about 18 inches; *C*, *Aulophyseter*, a Miocene sperm whale, skull length about 4 feet, jaw restored; *D*, *Cetotherium samarinense*, a Miocene whalebone whale, skull length about 22 inches. Abbreviations: *f*, frontal; *j*, jugal; *l*, lacrimal; *m*, maxilla; *n*, nasal; *p*, parietal; *pm*, premaxilla; *so*, supraoccipital; *sq*, squamosal. (*A* after Andrews; *B* after Abel; *C* after Kellogg; *D* after Capellini.)

telescoped effect, heightened by the fact that usually the occipital bones have pushed forward over the top of the skull. Apparently there is no top to the skull; it is all front and back.

The braincase has been much modified in shape in relation to these odd specializations and is short but broad and high. The orbit is always open behind, although typically covered by a broad supraorbital process of the frontal; and the jugal is small. The premaxilla of modern whales is usually toothless (there are small teeth in a few porpoises); the bone, however, is well developed on the skull roof. The ears are much changed for use in such "submarine" forms; the external tube and drum tend to be modified and reduced; and hearing, apparently acute (in contrast to the lost sense of smell), appears to be accomplished through the instrumentality of vibrations set up within the heavy, shell-like bulla, which, fused with the periotic, is but loosely attached to the remainder of the skull.

Whales may be divided into three suborders: the Archaeoceti, of the early Tertiary; and two living groups—the Odontoceti, or toothed whales, and the Mysticeti, or whalebone whales (Fig. 368).

Primitive whales.—The archaeocetes are the oldest and most primitive of the cetacean groups, first appearing in the Middle Eocene. Except for one North American specimen, all known types of that age are from northern Africa, suggesting that (like the subungulates) they may have originated on that continent. Many features of their structure suggest their origin as a branch of the primitive creodont stock which had taken up a fish-eating life, but a number of important modifications had already occurred in *Protocetus* and *Prozeuglodon* (Fig. 365, *A*) of the Upper Eocene. The snout was elongate (as in many fish-eating reptiles before them), and the nostrils had already accomplished half of their migration backward onto the top of the skull. In other respects, however, the skull was still much like that of a primitive creodont; there was a long, low braincase, and there was no trace of the telescoping of elements which was to be the most marked peculiarity of later whale skulls. The dentition, too, was essentially primitive; for, while the front teeth were peglike, the cheek teeth were still much like those of creodonts in appearance and the primitive placental tooth count of forty-four was not exceeded. But while the skull was still quite primitive, the body skeleton seems already to have advanced far in aquatic adaptations. Skeletal remains are rare; but by Upper Eocene times, if not earlier, the hind legs had been reduced to vestiges which did not project from the body. Obviously, the earliest whales were already more highly adapted to marine life than are the living seals, although the story of whale specialization was far from finished.

The peak of archaeocete development was reached in *Basilosaurus* (frequently termed *Zeuglodon* [Fig. 366]) and its relatives, which were widespread and common in the Upper Eocene seas. These were the giants among primitive whales. The long low skull (which reached a maximum length of 5 feet) was still primitive in many features, but the much compressed and serrated cheek teeth were departing further from the primitive carnivore type. While modern cetaceans are stockily built, some of the zeuglodonts were slim and elongate types which reached as much as 70 feet in length, with the proportions which modern imagination ascribes to sea serpents.

Basilosaurus and other primitive types did not, in general, survive the end of the Eocene. Of the archaeocetes, only some comparatively small, short-bodied forms—the *Dorudon* group—persisted in lessening numbers through the Oligocene and into the beginning of Miocene times.

Primitive toothed whales.—Odontocetes, or toothed whales, comprise the great majority of living cetaceans, ranging from small porpoises and dolphins to the huge sperm whale. The body is short and stocky, in contrast with the elongation in *Basilosaurus*. The teeth are usually simple pegs or wedges; are not differentiated into incisors, canines, and cheek teeth; and usually far exceed the primitive placental number (as many as three hundred in one porpoise). Most marked feature of specialization, however, is the extreme telescoping of the skull roof, mentioned above. The nostrils have moved far back over the top of the skull, forming a single vertically placed blowhole, unroofed by the reduced nasals. A backward elongation of the premaxillae and maxillae has accompanied this process. The maxilla has spread out sidewise over the frontal in a great shelf over the orbit and temporal region and, pushing the parietal entirely out of the mid-line of the skull roof, often comes in contact with the supraoccipital.

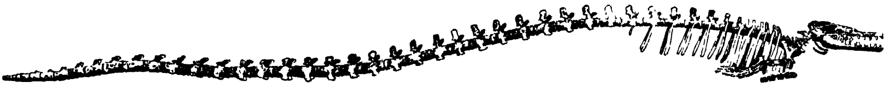


FIG. 366.—*Basilosaurus* [*Zeuglodon*], an archaic Eocene cetacean; original about 55 feet long. (From Gidley.)

No trace of this telescoping process is seen in the known archaeocetes. The toothed whales are presumably not derived from the elongate and temporarily successful zeuglodonts but may well have been derived from the earlier members of the archaeocete group. The development of the modern whale type proceeded rapidly. Two ancestral forms, of which *Agorophius* is the better known, appeared in Upper Eocene seas as contemporaries of *Basilosaurus*. The skeleton is unknown, but in their skulls they show definitely an early stage in the telescoping process; for, while there was little shifting of the occipital bones and the temporal region was still open above, the nostrils were already in position above the orbits and the maxillae were beginning to extend back and cover over the frontals.

These primitive forms appear to have been ancestral to the squalodonts, which, first appearing in the late Oligocene, became the characteristic world-wide cetaceans of early Miocene times. Such forms as *Squalodon* and *Prosqualodon* (Fig. 365, *B*) probably resembled greatly the modern porpoises in habits and appearance. These types owe their name to the triangular, shark-like teeth found in the posterior part of the beak (which was often much elongated). The squalodonts were much more modernized than their Eocene relatives, for the telescoping process in them had been completed, the parietals eliminated from the top of the skull, the maxillae had formed a contact with the supraoccipital, and the blowhole had reached its most posterior position above and behind the eyes. The temporal opening, however, had not yet been roofed over, as in many later odontocete types.

The squalodonts were not long destined to retain their importance, for only a single survivor lingered on into the Pliocene; and even by Middle Miocene times they had been largely replaced by other porpoise-like types.

Perhaps most closely related of living whales to the squalodonts are the long-beaked river porpoises of South America (*Inia*) and China (*Lipotes*). Here, as in most later odontocetes (and in contrast with squalodonts), all the teeth are simple peglike structures, and the premaxilla has tended to become toothless. But a primitive feature is found in the fact that in these porpoises, as in the squalodonts, the temporal opening is still unroofed. The living types are confined to the lower reaches of rivers, but their ancestors were undoubtedly sea dwellers; a number of presumed relatives were present in the Pliocene, and one even in early Miocene times.

Beaked whales.—While the squalodonts were the first toothed whales to attain prominence, other porpoise-like odontocetes became increasingly important during the Miocene. Among these forms are found the ancestors of the modern beaked whales, the Ziphiidae. In a modern beaked type, such as *Mesoplodon*, the "cow fish," the teeth have been lost except for one or two tusks in the lower jaw and nonfunctional vestiges in the maxilla. There are deep pockets on the top of the skull at either side of the blowhole. The temporal opening is roofed over by the maxilla in this family and in the remaining odontocete types considered; and, in addition, there is some asymmetry of the skull, a twisting of the elements about the blowhole. In modern members of this family, too, we find the beginnings of a fusion of the cervical vertebrae characteristic of the larger whales.

The beginnings of the beaked whales are to be found as far back as the early Miocene in the small dolphin, *Diochotichus*, which showed ziphioid characters in many respects but still resembled the squalodonts in the retention of a good set of teeth and in other primitive characters. True but primitive beaked types (such as *Choneziphius*) with a much reduced dentition were also developed during the Miocene, and by the end of that period the existing genus *Mesoplodon* had already appeared.

Porpoises.—The most numerous of living small cetaceans are those included in the family Delphinidae, the modern oceanic porpoises and dolphins and their relatives. They are advanced in such structural features as the completely telescoped skull and the temporal region. But in contrast to most other living whales, most delphinids have retained an efficient battery of teeth in both upper and lower jaws. The dolphins must have developed rapidly out of the primitive toothed whale stock, for forms essentially modern in build were not uncommon in the early Miocene when the squalodonts still flourished, and the family had become the most abundant group of odontocetes by Middle Miocene times. Commonest of Miocene types were such long-snouted forms as *Eurhinodelphis*, in which the rostrum made up four-fifths or more of the skull length. More modern porpoise types, such as *Kentriodon* (Fig. 367), appeared toward the close of the Miocene and in the Pliocene. Apart from the typical porpoises and dolphins, the family includes a considerable number of aberrant types, such as the killer whales, which prey upon seals, penguins, and even larger cetaceans, and the narwhal, with its "horn" formed from a sole remaining tooth. The slim-snouted *Platanista* of the Ganges River is probably a distant offshoot of the dolphins rather than a relative of the other river porpoises mentioned previously. It may have had a long separate history, however, for a type possibly related is known well back in the Miocene.

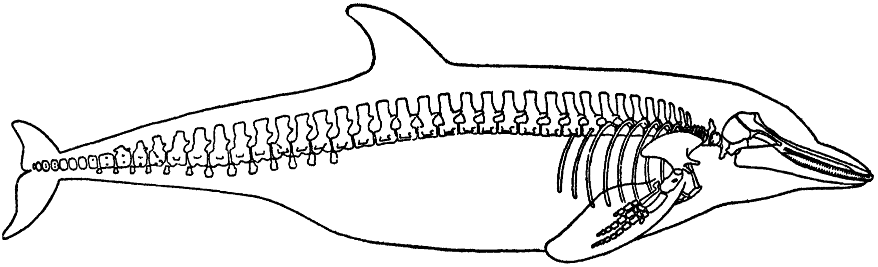


FIG. 367.—*Kentriodon*, a Miocene porpoise, about 5½ feet long. (From Kellogg.)

Sperm whales.—Largest of all odontocetes and exceeded among all animals only by certain whalebone whales is the living sperm whale, *Physeter*, type of the family Physeteridae. *Kogia*, the pigmy sperm whale, is a much smaller form. The huge snout of these whales is mainly occupied by a great reservoir of sperm oil; the upper jaws are slender and depressed, but farther back the skull rises to a great cross-crest cupping the hinder end of the sperm pocket. The asymmetrical twisting of the bone about the blowhole is especially noticeable in these forms, particularly in the greater backward expansion of the right premaxilla. In the upper jaw there are only a few functionless vestiges of teeth in the gums, but the lower jaw retains a complete and well-developed battery of teeth. In the postaxial skeleton a specialization lies in the fact that all the short cervical vertebrae are fused (with the exception of the atlas) into a solid mass. This feature is seemingly associated with the enormous head and repeated in some large-skulled whalebone whales. The living sperm whale had already appeared before the end of Miocene times. In earlier Miocene strata, however, are found remains of ancestral types. These were smaller, more primitive, and closer to the primitive porpoise stock, still retaining teeth in the upper jaw but with distinct evidences of the development of the pocket for the sperm-oil reservoir. *Aulophyseter* (Fig. 365, *C*) of the Middle Miocene is transitional between the older and the younger types.

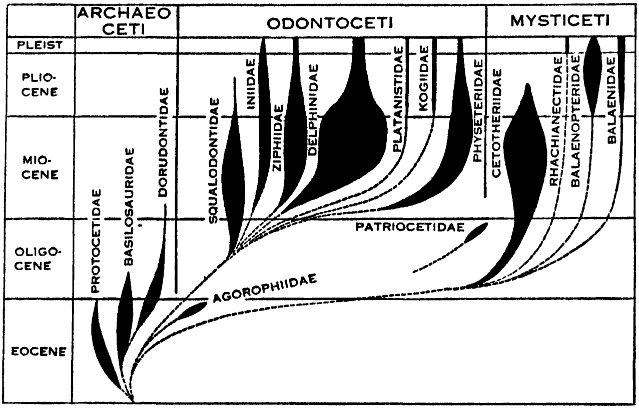


Fig. 368.—The phylogeny of the whales

Whalebone whales.—The Mysticeti, the whalebone whales, include but a small number of types, almost all of which, however, are of enormous size, including the largest of vertebrates, living or extinct. These greatest of cetaceans live on the smallest of prey, tiny floating invertebrates; it is impossible for such a whale to swallow any large object, for the gullet does not exceed 9 inches in width. Whalebone consists of ridges of hardened skin which extend down from the roof of the mouth in parallel crosswise rows like the leaves of a book. They are fringed at the edge with "hairs" upon which food particles catch, to be promptly licked off by the huge tongue. The teeth have been lost with the development of this peculiar apparatus; the mouth is enormously enlarged, the jaws bending out and down (and failing to meet in a symphysis), and the rostrum sometimes arched up. Telescoping of the skull has taken place in this group also, but in a somewhat different fashion from that of the toothed whales; for, while even in modern types the blowholes (here double) are still situated in front of the orbits, the normal roofing elements have been almost excluded from dorsal view by a forward migration of the supraoccipital region. The maxilla is braced against the frontal bone but does not override that element, although sending a finger-like process back over the skull roof. There is, in contrast with toothed whales, no trace of asymmetry.

It is obvious that these forms, now toothless, have descended from primitive toothed whales of some sort. One fragmentary late Eocene specimen, together with one or two Oligocene types such as *Patriocetus*, appear to show the beginnings of the type of skull telescoping which occurs in modern mysticetes. At all events, the history of the group had begun in the Oligocene with the first appearance of the cetotheres, primitive whalebone whales which were common forms in the Miocene and survived into Pliocene times. The cetotheres, including such forms as *Aglaocetus* and *Mesocetus*, were already toothless types in which telescoping was well under way. This process, however, had not progressed so far as in living types, for dorsally a considerable gap still existed between the backward, finger-like process of the maxilla and the supraoccipital.

Representatives of the two living families were in existence by Miocene times. Of these families, one includes the rorquals (*Balenoptera*) and their relatives—types with small skulls, free cervical vertebrae, and a low and broad rostrum. The other family includes the right whales (*Balaena*), now confined to Arctic and Antarctic regions, forms with large skulls, fused cervicals, a curved rostrum, and a deep jaw. Of the rorquals, the blue or sulphur-bottom whale is estimated to reach a maximum weight of 150 tons or more, thus being far larger than any dinosaur.

CHAPTER 26

RODENTS

AMONG the gnawing animals—the order Rodentia—are included the squirrels and beavers, rats and mice, porcupines and guinea pigs, and hosts of less familiar forms. The rodents are, without question, the most successful of all living mammals. In number of genera and species they exceed all other orders combined; they are found in almost every habitable land area of the globe and seem to thrive under almost any conditions, flourishing even in man-made towns and cities. The range of adaptations is a wide one. A majority of rodents are terrestrial and often burrowing types. No purely aquatic forms have developed, but such forms as the beaver and muskrat have progressed far in this direction. Others, like the squirrels, are arboreal; and while there are no flying rodents, the "flying" squirrels have tended in this direction.

In size the rodents are a modest group. Most forms are small, and the rat or squirrel may be taken as an average; the capybara of South America, the size of a pig, is the giant of the group.

Dentition.—The rodents are essentially herbivores, although certain of them, such as the rats, will accept a wide variety of food; the peculiar gnawing and grinding dentition and adaptations related to its use are highly characteristic of the group. A single pair of incisors is present in the lower jaw, and it is opposed by a principal pair above. These huge teeth never form roots and have bases which curve far back inside the bones of the upper and lower jaws; their continual growth counterbalances the wear to which they are subjected in gnawing. The other incisors, the canines, and a number of premolars have been lost in all known rodents, leaving a long diastema between the gnawing teeth and the grinding series. There are never more than two upper premolars and a single lower one, and in many of the modern ratlike forms only the molars remain in the cheek region. The cheek teeth often become high crowned, and in many cases they fail to close their roots and, like the incisors, continue to grow throughout life. The two upper rows of grinders are closer together than the lower ones and are tilted so that they meet the lower teeth in a plane that faces somewhat outward as well as downward.

The rodent molar pattern appears primitively to have followed the general mammalian herbivore tendency toward the development of rectangular, four-cusped cheek teeth, and in a few cases a simple pattern readily interpretable in terms of familiar placental cones has persisted; usually, however, such interpretation is difficult, and a wide degree of variation exists, even within the limits of single families. Much of this variation is associated with the development of high-crowned teeth which tend to be formed of a complicated series of ridges. These often become united as the tooth is worn; the original boundaries may be indicated by grooves and loops in the enamel pattern or may be completely obliterated in the formation of peglike structures.

A molar pattern found in some members of all major rodent groups and perhaps antecedent to many of the more complicated types is that illustrated in Figure 370. The shape is roughly that of the letter E. Three transverse ridges project laterally in the upper molar; the anterior and posterior ridges are formed primarily by paracone and metacone; the intermediate one is a newly developed mesoloph. Additional cross-lophs may be formed anteriorly and posteriorly from cingulum upgrowths or by elaboration and subdivision of those already present. Toward the medial side are protocone and hypocone, frequently separated by a marked furrow; a new mesocone appears between them on the longitudinal crest of the tooth. The lower molar develops in comparable fashion.

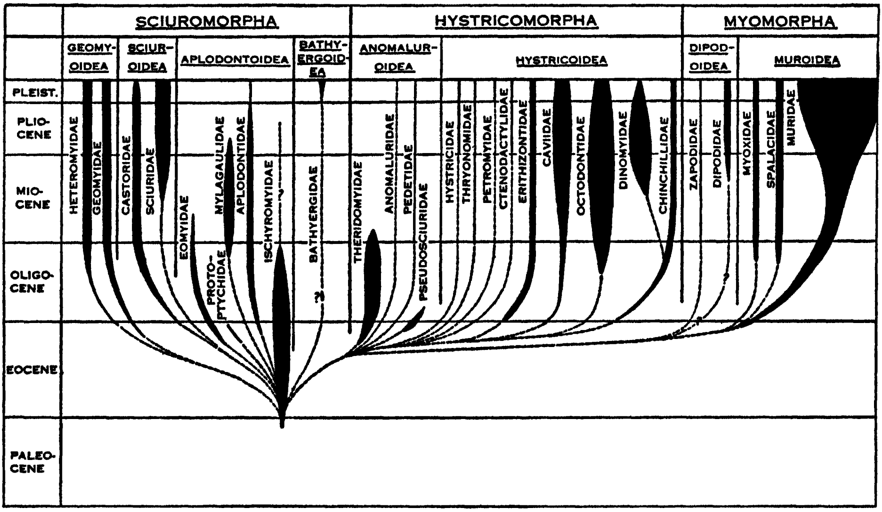


FIG. 369.—The phylogeny of the rodents

Skeleton.—With these adaptations for grinding and gnawing has come a series of peculiar adaptations in the skull and jaws. In most rodents there occur both fore-and-aft and transverse grinding movements of the lower jaws on the skull. In consequence the glenoid fossa of the skull (in which the lower-jaw condyle is received) is long and shallow, permitting considerable freedom of motion. The rodent skull is usually long and low, the orbit always open behind.

There are comparatively few specializations in the postcranial skeleton. The clavicle is usually retained; claws are always present. The front leg is usually flexible and often used as an aid in bringing food to the mouth, and there is little tendency toward loss of digits in the manus except for the occasional reduction of the pollex. The hind leg, however, is less flexible in its movements and confined to a fore-and-aft motion; tibia and fibula often fuse distally, and there are varying degrees of reduction of the toes with the development of a hopping or springing type of locomotion.

Major criteria in rodent classification lie in skull modifications related to the jaw musculature. In addition to the temporal muscles closing the jaw, all mammals possess another series termed the masseters. These primitively pass from the zygomatic arch downward to the outer surface of the mandible (Fig. 371). In rodents the masseters consist of two sheets, lateral (superficial) and medial (deeper); these are highly developed to give the fore-and-aft and rotary movements of the jaw characteristic of the order. Various modifications of these muscles may occur. In advanced sciuromorphs and myomorphs the lateral masseter may push forward at its origin and extend upward onto the side of the rostrum in front of the orbit. The medial masseter may likewise become specialized. In primitive mammals an opening—the infraorbital canal—runs forward from the orbit carrying small nerves and blood vessels onto the side of the snout. This canal may become much enlarged, and the origin of the medial masseter pushes upward through the orbit and forward through this canal in hystricomorphs and myomorphs.

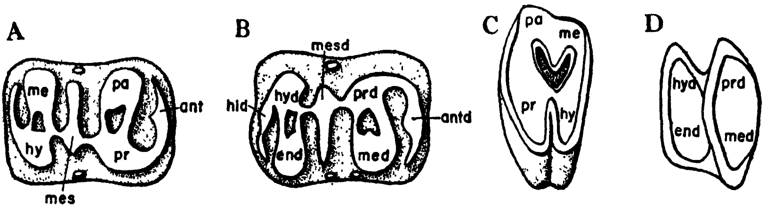


FIG. 370.—Diagrams of molar patterns in rodents and lagomorphs, *A*, *B*, Right upper and left lower molars of a type common in rodents (particularly myomorphs); *C*, *D*, right upper and left lower molars of lagomorphs. Abbreviations: *ant*, Anterocone; *antd*, anteroconid; *mes*, mesocone; *mesd*, mesoconid. For other abbreviations see Figure 241, with which these patterns may be compared. (After Wood and Wilson.)

Classification.—So numerous and varied are the rodents, living and fossil, that no two authors agree on their classification. It is generally conceded that the squirrels, the rats, and the porcupines are representative of three distinct groups, generally considered as suborders—Sciuromorpha, Myomorpha, and Hystricomorpha. There are, however, numerous families and groups of families, both living and fossil, which do not fall readily into these categories; actually there are perhaps eight or more natural assemblages of rodent families. We may, nevertheless, squeeze them somewhat arbitrarily into the classic framework by keeping the rat and porcupine suborders for important terminal groups and using the sciuromorph category as a "dumping-ground" for a number of primitive and variously specialized but relatively small groups, as follows:

Suborder Sciuromorpha: superfamilies Aplodontoidea, Sciuroidea, Geomyoidea, Bathyergoidea.

Suborder Hystricomorpha: superfamilies Anomaluroidea, Hystricoidea.

Suborder Myomorpha: superfamilies Dipodoidea, Muroidea.

Primitive sciuromorphs.—It is generally agreed that the Sciuromorpha is the most primitive of the three groups and that the other two have probably been derived from primitive squirrel-like forms. Only in the sciuromorphs are two upper premolars and a lower premolar present, and even here the anterior upper one is small and often lost. A characteristic feature is the comparatively primitive position of the masseteric muscle. In no sciuromorph, as here defined, is the infraorbital canal enlarged for the medial masseter, and in the more primitive forms the lateral masseter is likewise unspecialized.

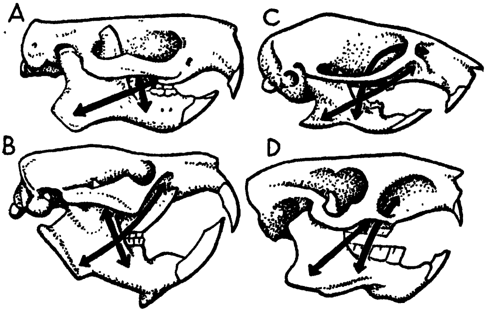


Fig. 371.—Diagrams to show the development of the superficial and deep portions of the masseteric muscle in various rodent types. *A*, A primitive sciuromorph; the masseter originates mainly from the lower edge of the zygomatic arch. *B*, An advanced sciuromorph; the superficial masseter originates from the outer side of the skull in front of the orbit, *C*, A myomorph; the superficial masseter is similar, but the deeper portion has pushed up through the orbit and arises in a pocket on the face, formed from the infraorbital foramen. *D*, A hystricomorph; the superficial masseter is unspecialized, but the foramen is enormously developed to accommodate the deeper portion.

Aplodontoidea.—Perhaps the most primitive of living rodents is *Aplodontia*, the sewellel, or "mountain beaver," of the American Northwest. In this small ground-dwelling rodent the skull is long and low, the brain small, and the braincase is not swollen. There is not even a trace of a postorbital process of the frontal bone, and the masseter attaches to the zygomatic arch in primitive fashion.

We may associate with the sewellel, as constituting a superfamily Aplodontoidea, a great series of primitive rodents, such as *Paramys* (Figs. 372, *A;* 374; 375) and *Ischyromys* (Fig. 373, *A*), which flourished in the northern continents, particularly North America, in Eocene and Oligocene times. Many of these rodents were rather squirrel-like in size and proportions and, very possibly, in appearance and habits as well. The cheek teeth were, in general, still low crowned and exhibit patterns which in some cases are fairly comparable to normal quadritubercular teeth seen in other orders. The ischyromyids are the oldest of known rodents; but, although primitive in many ways, they were already definitely true rodents and give us little in-

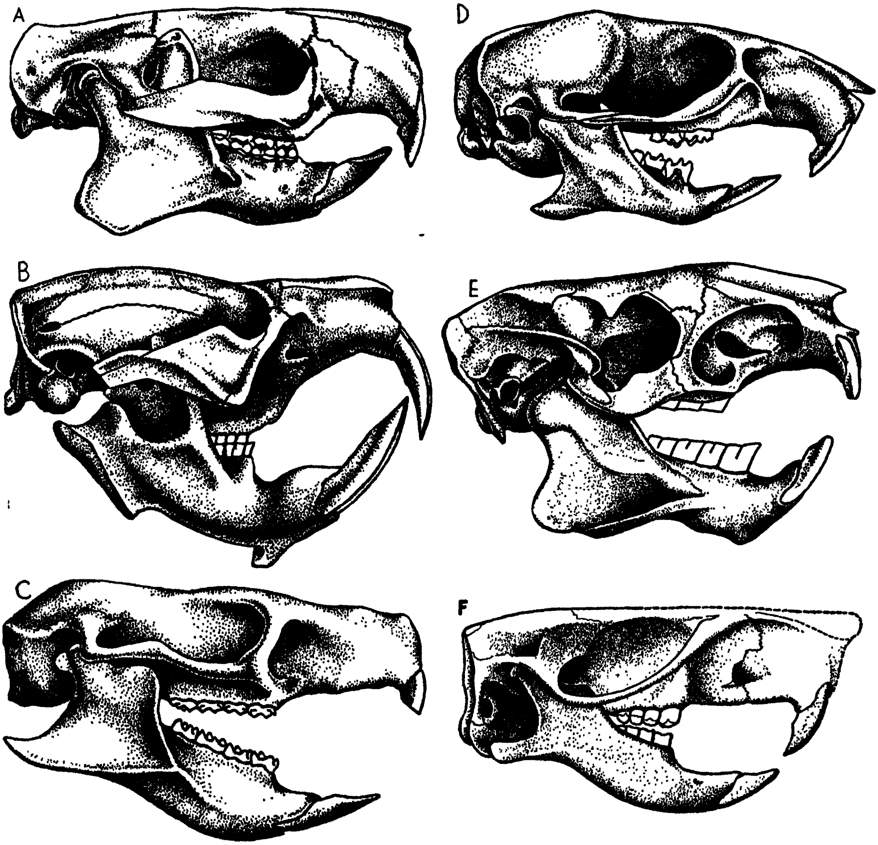


Fig. 372.—Skulls of rodents. *A*, *Paramys*, a primitive sciuromorph, skull length about 3½ inches; *B*, *Palaeocastor*, a Lower Miocene castorid, skull length about 2¾ inches; *C*, *Pseudosciurus*, an Eocene anomaluroid, skull length about 2⅓ inches; *D*, *Cricetops*, a Tertiary murid, skull length about 1 inch; *E*, *Neoreomys*, a Miocene South American hystricomorph, skull length about 4 inches; *F*, *Florentiamys*, a Miocene geomyoid, about natural size. (*A* after Matthew; *B* after Peterson; *C* after Schlosser; *D* after Schaube; *E* after Scott; *F* after Wood.)

dication of the early stages by which this order arose from the primitive placentals.

From the ischyromyid group were surely derived the sewellels; members of the Aplodontidae had appeared in North America before the close of the Eocene, and a series of forms leading to the modern genus are present in later American Tertiary deposits. An early specialized side branch includes some Middle Tertiary American forms such as *Mylagaulus*, in which the last premolar became enormous and the molars reduced, and *Ceratogaulus* and its relatives, which alone among rodents had horns (in the male at least). Still further early offshoots of the ischyromyids include *Eomys* and *Protoptychus* of the Eocene and later Tertiary relatives of the former. More important is the fact that the early time of appearance and primitive structure of the ischyromyids suggests them as possible ancestors of all the varied rodent groups, myomorphs and hystricomorphs as well as the remaining sciuromorph types.

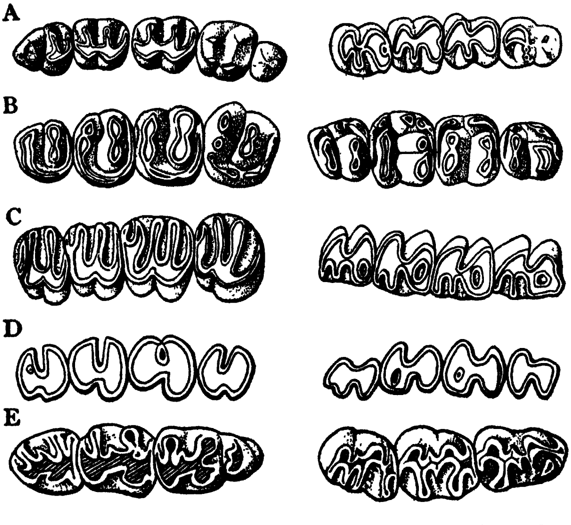


FIG. 373.—Teeth of rodents. *Left*, upper cheek teeth of right side; *right*, lower cheek teeth of left side. *A*, *Ischyromys*, a primitive Oligocene sciuromorph (×$\frac{7}{2}$); *B*, *Florentiamys*, a Miocene geomyoid (×5 approx.); *C*, *Theridomys*, an early Tertiary anomaluroid (×6 approx.); *D*, *Sciamys*, a Miocene South American hystricoid (×$\frac{9}{2}$); *E*, *Eumys*, an Oligocene murid (×5 approx.); (*A*, *E* after Matthew; *B* after Wood; *C* after Schlosser; *D* after Scott.)

Squirrels and beavers.—A second group of sciuromorphs is that here considered as constituting the superfamily Sciuroidea—the squirrels and beavers and related types. A diagnostic feature separating them from the aplodontoids lies in the fact that the lateral head of the masseter arises from a prominent channel lying anterior to the zygomatic arch and extending far up the side of the rostrum (Fig. 371, *B*). The more primitive family is that of the squirrels, the Sciuridae. These amiable creatures are in most respects relatively unspecialized; the teeth are almost always low crowned and of primitive pattern, and the small third upper premolar is usually retained. The main group of squirrels are arboreal forms, with the "flying" squirrels of the Northern Hemisphere as an offshoot. Others, as ground squirrels, have become primarily terrestrial, including such forms as the "gophers" and chipmunks. A group of large, short-tailed burrowing forms includes the prairie dog, common on the western American plains, and *Marmota* [*Arctomys*], the woodchuck or marmot, common as a fossil in the colder phases of the European Pleistocene. *Sciurus* and other members of the family, presumably derived from the early Tertiary ischyromyids, appeared in the Miocene and spread widely in Eurasia and North America. They never reached Australia but successfully invaded South America in the Pleistocene.

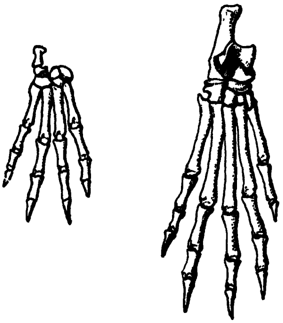


FIG. 374.—Right manus and pes of *Paramys*, an Eocene sciuromorph rodent. (After Matthew.)

The Castoridae, of which the beaver is the only living representative, are sometimes placed in a separate superfamily; but they appear to be, for the most part, merely squirrel-like forms which have tended to grow to large size, with accompanying specializations. The small third upper premolar has disappeared in castorids, resulting in a battery of four cheek teeth both above and below in these rodents (and in nearly all the remaining sciuromorphs and hystricomorphs). The cheek teeth have become hypsodont, presumably in correlation with large size and increased grinding requirements, a feature repeated in many other rodent types. A further specialization also encountered in other progressive groups is the fusion of tibia and fibula.

The beaver, *Castor*, is an aquatic type, and this mode of life may well have been present in some of the older castorids, the first of which appear in the Oligocene. Some, however, were burrowers. *Palaeocastor* (Fig. 372, *B*), *Steneofiber*, and their relatives are common Miocene fossil rodents in both Europe and North America; in western Nebraska peculiar upright "devil's corkscrews" found in the Lower Miocene beds have been thought to be their mud-filled burrows. Giant beaver types were found in both northern continents in the Pleistocene; *Castoroides* (Fig. 376) of North America attained the size of a half-grown bear; *Trogontherium* was a large European form.

Geomyoids.—Also included in the sciuromorphs is the superfamily Geomyoidea (Figs. 372, *F*; 373, *B*), a purely American assemblage containing the mouselike kangaroo rats (Heteromyidae) and the larger burrowing pocket gophers (Geomyidae), both of which occur in that continent from Oligocene times on. From a low-crowned condition in the Oligocene ancestors, the teeth have gradually become high crowned and, in the pocket gophers, rootless. Here, again, tibia and fibula are fused. The pocket gophers are burrowing types which owe their name to the large cheek pouches; the kangaroo rats are small, hopping desert rodents with elongate hind legs. This is the first of several similar hopping types of rodents which have evolved independently in various groups.

Bathyergoids.—We here include in the sciuromorphs, for want of any better place to put them, the Recent *Bathyergus* and its relatives, aberrant subterranean burrowing rodents from Africa. Except for a few doubtful forms from the Old World, their history is unknown. They are sometimes associated, rather dubiously, with the hystricomorphs because they show an out-turned angular region of the jaw seen in characteristic members of that suborder. There are, however, no other features suggesting such relationships, and the diagnostic masseteric structures are of the primitive type seen only in the early sciuromorphs. We may best regard them as an early specialized offshoot of the primitive sciuromorph stock, not closely related to any other group.

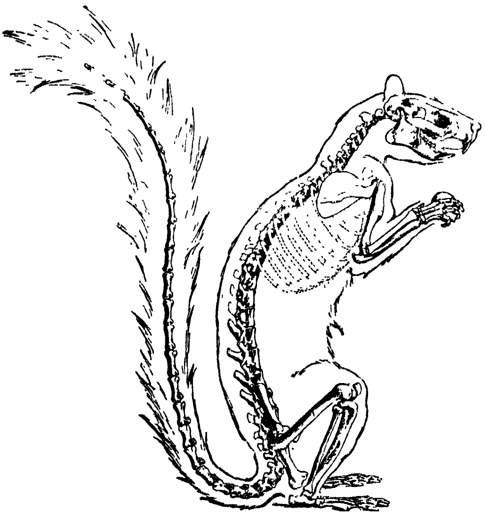


FIG. 375.—*Paramys*, a primitive Eocene squirrel-like rodent; original about 16 inches high in sitting pose. (From Matthew.)

Anomaluroids.—One of the most perplexing but phylogenetically interesting groups of rodents is the superfamily Anomaluroidea, including among living types only a few African genera; *Anomalurus*, resembling a flying squirrel, and *Pedetes*, the "Cape jumping hare," are representative. These rodents exhibit primitive features which have caused many to include them in the sciuromorphs. They show, however, one progressive character not found in any member of that suborder—a large infraorbital canal through which the medial masseter has pushed from the orbit forward onto the side of the snout. Such a structure is present in both myomorphs and typical hystricomorphs, and hence many writers have suggested placing the anomaluroids in one or the other of these groups. The myomorphs, however, have additional dental and cranial specializations not found in anomaluroids;

their absence indicates that the anomaluroids cannot properly be considered as Myomorpha. On the other hand, tne typical hystricomorphs differ but little from the anomaluroids. We therefore include the latter in the suborder Hystricomorpha, broadly defined as showing specialization of the medial, but not the lateral, masseter and as retaining the "normal" set of four cheek teeth in each jaw ramus. It may well be, however, that all three points of view on the position of anomaluroids are partially true and that they represent a stock which developed out of the early sciuromorphs and gave rise to both the typical hystricomorphs and the myomorphs. The fossil record is in harmony with this belief. The existing families are poorly represented in the fossil record. We find, however, in the late Eocene of Europe and in the Oligocene and Miocene of Africa a considerable number of small rodents presumably lacking the specializations of the living anomaluroids but with the same type of construction of the infraorbital canal. These forms, such as *Pseudosciurus* (Fig. 372, *C*) and *Theridomys* (Fig. 373, *C*), appear to be transitional in character between the primitive *Paramys* type and the typical hystricomorphs and may be close to, if not on, the line leading to the myomorphs as well.

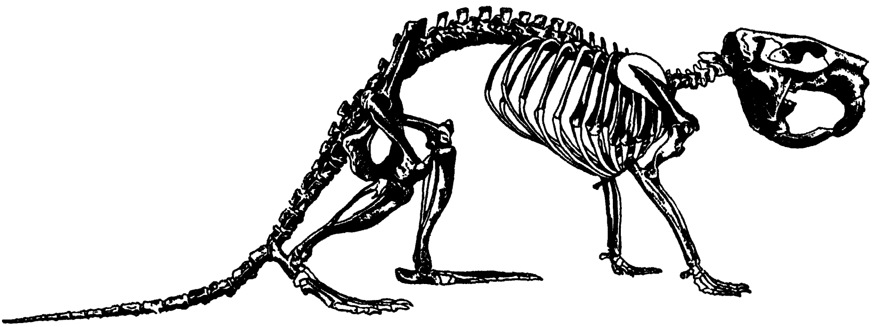


FIG. 376.—*Castoroides*, a giant beaver, about 7½ feet in length, from the Pleistocene of North America

Typical hystricomorphs.—One of the most important of existing rodent groups is that of the hystricoids, the typical members of the suborder (Figs. 372, *E*; 373, *D*). As in the anomaluroid types, the infraorbital opening is greatly enlarged for the medial masseter, while the lateral element of that muscle retains its primitive position (Fig. 371, *D*), and four well-developed cheek teeth are present. An additional diagnostic feature, however, lies in the fact that the angular region of the lower jaw typically develops as a prominent out-turned horizontal ridge for masseteric insertion.

The present geographical distribution of the hystricoids is a peculiar one. A minor center lies in Africa, where there are porcupines of the *Hystrix* type and a few other forms, such as the cane "rat," *Thryonomys;* the porcupines are also present in Eurasia. A much more important center is South America. North America has no hystricomorphs except the porcupine *Erethizon*, a Pleistocene immigrant from the south which is not at all closely related to Old World porcupines. South America, on the other hand, is an exclusive hystricomorph territory, save for a number of rats and a few sciuromorphs which were Pleistocene invaders.

There is no general agreement as to the proper arrangement in families of the numerous hystricoids of that continent. We have here "lumped" them in five families, though several of these are presumably worthy of subdivision. The Octodontidae have, in general, a rather ratlike build, with a slender body, short legs, and a long, slim tail. In some, such as *Octodon* and *Echimys*, the general appearance is quite ratlike; *Abrocoma* is a furry form; the tuco-tuco (*Ctenomys*) is a burrower somewhat analogous to the pocket gophers; *Myocastor*, the coipu, is a large "water rat." A second large assemblage is that of the Caviidae, stockily built, stub-tailed rodents. The guinea pig or cavy (*Cavia*) is a representative of modest size; larger types tend to be rather ungulate-like and include the paca (*Coelogenys*) and the capybara, *Hydrochoerus*, the giant among living rodents, with a body length of 4 or 5 feet. The Erethizontidae are the New World porcupines. The Chinchillidae include a small number of furry, bushy-tailed, and somewhat squirrel-like burrowers. We have placed in a separate family *Dinomys*, a rather large rodent with peculiar high-crowned cheek teeth, formed, like those of the chinchilla, of parallel laminae.

The geological history of the hystricoids reveals a distributional picture similar to that seen today, with a major concentration in South America and a minor sprinkling of fossils in the Old World Tertiary, mainly in Africa.

Hystricoids first appear in South America in the Oligocene, suddenly and in considerable variety, for almost all modern groups are represented at that time, and by the Pliocene they had become very numerous and diversified. Notable in the Pliocene is the development of forms of large size in several lines. By the Pleistocene a variety of hystricoids, some of the caviid group, and others perhaps related to *Dinomys* had found access to the West Indies; only a few have survived. Some of these insular forms were of large size; the giant of fossil rodents, however, was the mainland genus *Eumegamys*, with a skull close to two feet in length and a bulk presumably comparable to that of a wild boar. The hystricoids do not appear to have been seriously reduced by the Pleistocene invasion of South America from the north. On the other hand, except for the porcupine, they made little progress toward an invasion of the north, although the capybaras reached the Gulf states in the Pleistocene.

In the Eastern Hemisphere there are records of fossil porcupines from the late Cenozoic of Eurasia; in Africa there have been found a few fossil hystricoids and, in addition, a number of forms which may be transitional between early anomaluroids and hystricoids. If the group were confined to the Old World, we might reasonably and simply explain their origin as from the anomaluroids with Africa as the locale. But their presence in South America is quite another matter. They appeared there in the Oligocene. At that time that continent had been completely isolated from other regions, we believe, for at least a full epoch. It is difficult to believe that such a potentially successful group had entered long before and yet escaped the fossil record; and, furthermore, there are no North American rodents which look like possible candidates for hystricoid ancestors. It is highly improbable that any land connection existed between South America and Africa at any stage of the Tertiary because of the absence of intermigration of other elements in the mammalian fauna. It is, however, hard to escape the conclusion that the hystricoids, by some means or other, made a successful western crossing of the South Atlantic.

Primitive myomorphs: the jerboas.—A highly specialized group of living rodents which shows characters transitional between the anomaluroid type of structure and that seen in typical members of the rat-mouse group includes the jerboas (*Dipus* and various other Old World genera) and the related jumping mouse, *Zapus*, of North America. These are small desert dwellers, most of which (like the kangaroo rats) have assumed a hopping gait. There are, naturally, adaptations related to their mode of life. The front limbs are much reduced; the hind legs are peculiarly birdlike in structure, for there are three symmetrical toes whose metapodials are fused into a single elongate element.

The skull and jaw structures are basically much like those of the anomaluroids, including the presence of a much enlarged infraorbital canal; some specialists on the order have tended to associate them with these forms, and it is quite possible that the jerboas (and the typical myomorphs as well) have arisen from some of the early fossil types here included in the anomaluroids. There are, however, numerous features indicating relationship with the rat tribe. We may cite as an example the cheek teeth. In typical muroids these are reduced to the three molars alone, of which the first are much larger than the more posterior ones. In jerboas an upper premolar persists but is very small, and the lower premolars have vanished; and in the molar series the first is already much larger than its neighbors. Fossil dipodoids are rare, although a few are found in Eurasia as far back as the Oligocene. The dipodoids may be regarded as a specialized offshoot from the base of a line leading to the more progressive myomorphs.

Muroids.—The remaining, more characteristic myomorphs may be placed in a single broad superfamily, the Muroidea. In these forms (Fig. 371, *C*) the infraorbital canal is enlarged for the transmission of muscle as in hystricomorphs and the jerboas. A second change has, however, occurred in this region, for the lateral masseter has excavated a channel for itself up the front of the zygomatic arch in a fashion parallel to that of sciuromorphs.

A primitive muroid family is that of the dormice, or sleepers, of which *Myoxus* [*Glis*] is typical. These small, arboreal fruit-eaters are more primitive than ordinary mice and rats in their cheek teeth. These remain low crowned and rooted; and a condition even more primitive than that of the jerboas is seen in the retention of a small premolar in lower, as well as upper, jaw. The dormice are exclusively Old World forms, first recognized in the Miocene.

Very specialized muroids are the burrowing-rat types, *Spalax* and *Rhizomys*, with an Old World pedigree dating back to the Oligocene. In basic features they are very close to the typical rats and mice, but there are numerous adaptive features which entitle them to recognition as representatives of a distinct family (or families).

The remaining muroids are here included in a single comprehensive family of rats and mice—the Muridae (Figs. 372, *D;* 373, *E*). In these rodents the last premolars have disappeared, the molars (the first usually much larger than the others) taking over the entire burden of grinding. In the more primitive genera the teeth are low crowned and rooted; in others there is a development of high-crowned, rootless teeth.

The murids are an old and highly successful group. The first definitely recognizable genera date from the Oligocene, but it is not until the Pliocene that they become common. In late Cenozoic and Recent times they have become the most widespread and abundant of rodents—indeed, of all mammals. Recent murids outnumber all other rodents in the number of genera and species and, it seems certain, in the number of individuals as well, and their dominance in Pliocene and Pleistocene days was nearly as great as now. Their geographical range is greater than any other rodent group, for they not only invaded South America when that continent became readily accessible in the Pleistocene but are also present in Australia, a region to which no other terrestrial placentals were able to make their way before the coming of man. Two major groups of murids are often distinguished—the Cricetinae and Murinae (sometimes treated as separate families). The center of murid evolution appears to have been the Eastern Hemisphere, but the cricetines have been present in North America since the Oligocene, and they constitute the entire native assemblage of rats and mice. The murine division is native to the Old World tropics, but in recent times the common mouse (*Mus*) and rat (*Rattus*) have accompanied man to all corners of the world.

Lagomorphs.—The hares and rabbits were long considered as a suborder of the rodents (the Duplicidentata); but, apart from the fact that they have gnawing incisors and grinding cheek teeth, they have little in common with the rodents and are now regarded as constituting a separate order Lagomorpha.

As in true rodents, the functionally important gnawing teeth are a single pair of incisors above and below, but in the lagomorphs an accessory pair of small upper incisors is present behind the principal ones. There is, as in rodents, a long diastema; the outer incisors, canines, and some premolars have been lost in its development. The number of cheek teeth present is higher than in any rodent, for there are always three upper premolars and two lower ones in addition to three molars. The cheek teeth (Fig. 377) are high crowned and rootless, with patterns presumably derived from those seen in early placentals. The upper molars seem basically comparable with the primitive tritubercular pattern; the lower ones have, as in many other groups, developed two cross-lophs. In contrast with rodents, the two upper tooth rows are farther apart than the lower ones, and the teeth have more of a chopping than a grinding motion. There is never any enlargement or muscular invasion of the infraorbital canal. A peculiar lattice-work fenestration of the side of the snout is a noticeable feature of the lagomorph skull. The tail is short or absent in all known forms.

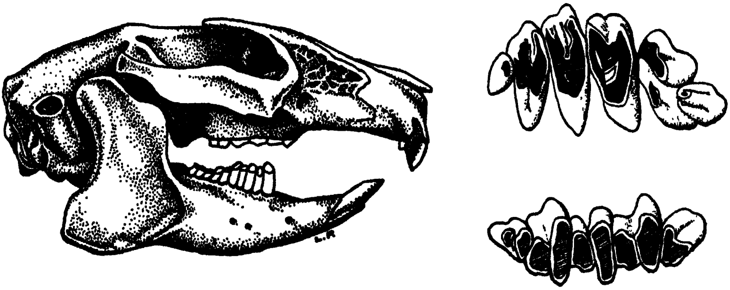


FIG. 377.—*Palaeolagus*, an Oligocene hare; skull, right upper and left lower cheek teeth; skull about 2 inches in length; teeth ×4 approx. (After Troxell and Wood.)

Best known of the group are the leporids, including the living hares (*Lepus*) and rabbits (*Oryctolagus*) and their relatives, leaping forms with much-elongated hind legs. A less prominent type is that represented today by the pika, *Ochotona*, of the mountains of western America and Asia, with short legs and short ears. Fossil hares are known in both Eurasia and North America as far back as the late Eocene and the Oligocene, when *Palaeolagus* (Fig. 377) was apparently not uncommon in North America. The pikas, before the Pleistocene, appear to have been an Old World group whose earliest-known appearance was in the Oligocene.

Until recently no earlier representatives were known. It now appears, however, that the incompletely known *Eurymylus* from the late Paleocene of Asia is an ancient lagomorph, although the loss in this genus of a small premolar debars it from a strictly ancestral position. As far as their structure is known, the older lagomorphs appear already to have acquired the typical features of the order and show no evidence of particularly close relationship to other placental groups.

The hares and rabbits are a flourishing group, although their history has been confined almost entirely to the northern continents. They never reached Australia; but their all-too-successful career there since their artificial introduction is a well-known story.

CHAPTER 27

VERTEBRATE HISTORY: INTRODUCTORY

PALEOZOIC VERTEBRATES

IN PREVIOUS chapters we have considered the history of the various vertebrate groups with especial regard to structure and phylogeny. In the present chapter and in chapters 28 and 29 we shall review briefly the knowledge thus gained in a discussion of the faunal succession of the vertebrates, their distribution in time and space.

Geologic periods.—The conventional subdivisions of geologic time—eras and periods—have, in general, been established on the basis of events n the marine waters of Europe and North America; and boundaries between periods were set up at points where there appeared to be major breaks in the record of deposition or marked changes in the invertebrate life. But it is obvious, a priori, that a break in the record of sedimentation in one region by no means proves that a similar cessation will appear in others, and it becomes increasingly apparent that sharp lines of demarcation do not in reality exist. Furthermore, a comparatively sudden change in marine invertebrates by no means implies a marked simultaneous change on the continents, and many of our most interesting vertebrate faunas lie on the border line between periods or even eras. The earliest Devonian vertebrates, for example, are more like those of the late Silurian than like later Devonian fishes; the late Pennsylvanian tetrapods are almost identical with those of the Lower Permian. We cannot, however, readjust the period boundaries to suit the vertebrates alone, and we may retain the current nomenclature, while recognizing its artificiality (cf. Table 1).

Correlation of deposits.—In assigning an age to vertebrate-bearing beds, the evidence obtained from associated invertebrates is exceedingly useful. Many of the more important deposits, however, are of continental origin and contain almost no invertebrate remains. Here recourse is often had to a direct comparison with vertebrates of other regions. If two series of deposits contain a considerable number of identical or closely related forms, it is highly probable that they are contemporaneous. But if the forms compared are few in number or but distantly related, the argument for contemporaneousness is greatly weakened.

Negative evidence.—Any contrast between the life of different periods or different geographical areas is based upon the presence at one time or place of animals apparently absent at an earlier or later date or from another region. But it must be pointed out that, while the presence of an animal may be definitely shown, absence is incapable of absolute proof; all that we can really say is that remains have not been discovered. Until recent decades no placental mammal had been identified in collections from the Cretaceous. But our knowledge of later mammalian evolution led us strongly to believe, despite this negative evidence, that there must have been Mesozoic placentals. Today, principally owing to work in Mongolia, placentals are known in the Cretaceous. Negative evidence of absence has been replaced by positive knowledge of the presence of these forms. Again, no trace of coelacanth crossopterygians has ever been discovered in Cenozoic strata; and it was long believed, with confidence, that the coelacanths had become extinct at the end of the Cretaceous. The recent discovery of a living specimen has rudely shattered this belief.

TABLE 1*

TABLE OF GEOLOGIC PERIODS

ERA	PERIOD		APPROXIMATE TIME (IN MILLIONS OF YEARS)	
			Duration	Since Beginning
Cenozoic (age of mammals and man)	Quaternary		1	1
	Tertiary		69	70
Mesozoic (age of reptiles)	Cretaceous		50	120
	Jurassic		35	155
	Triassic		35	190
Paleozoic (age of invertebrates and primitive vertebrates)	Permian		25	215
	Pennsylvanian	Carboniferous	35	250
	Mississippian		50	300
	Devonian		50	350
	Silurian		40	390
	Ordovician		90	480
	Cambrian		70	550

* The older eras, in which vertebrates are unknown, are not included.

It is probable that the range in time or space of many forms with which we are familiar was greater than is now known. It is further probable that there may have existed many interesting vertebrate types of which no remains have as yet been discovered. But such probabilities are decreasing as our knowledge expands. During the present century a very great amount of paleontological work has been done, and many strange forms have been brought to light. These, however, have been almost always members of groups already known or forms tending to connect such groups.

Environmental differences.—In a study of past faunas the great variety of possible habitats must be taken into consideration. Often the structure of an animal gives much evidence concerning its environment. The teeth may afford a basis for distinguishing between forest-living browsing types and plains-dwelling grazers; the limbs may show us whether we are dealing with an aquatic, terrestrial, arboreal, or aerial form. The nature of the sediments and the associated plants and invertebrates may give us important additional information as to its surroundings in life or death.

Among fishes the question of a fresh- or salt-water habitat is often of great interest. If a fossil type is found in strata in which marine invertebrates do not occur, it is not unreasonable to assume that it inhabited fresh waters. If it is accompanied by such invertebrates, it may well be a marine form; but this is none too certain if the association is a rare one or if the vertebrate remains are badly broken, for individuals of a river-dwelling type may drift out and become buried in the sea.

Among land animals, distinctions may be made between lowland and upland types, forest and plains dwellers. Here an unfortunate difference in the probability of preservation appears. Wooded areas are obviously regions in which but little deposition of sediments takes place and in which skeletons are usually rapidly destroyed by insects or by acids in the soil. Hence our knowledge of the evolution of arboreal and forest-dwelling animals is relatively meager; in contrast, deposits are common in plains areas and skeletons often preserved. Of the evolution of primates and raccoons we know little; horses and dogs, mainly dwellers in open country, are abundant as fossils. Deposition has been common in coastal lowlands, but highland regions are areas of erosion; in consequence, our knowledge of the evolution of upland forms is slight.

Climates.—At the present time differences in temperature are a major factor in the distribution of vertebrate life. Many groups are confined to the tropics, others to arctic or temperate regions. This zonal distribution forms an effective check to migration. Penguins presumably would flourish in the arctic regions, polar bears in the south; but they cannot cross the tropics. The animal life of Old and New World tropics differs greatly, for intermigration in the more recent geological epochs necessitated a passage through the arctic zone. Similar situations may have strongly influenced the migration and distribution of vertebrates in the past.

Ancient climatic conditions, however, appear to have varied greatly. There is considerable evidence suggesting warmer climates at times in the past in regions now in the temperate or arctic zones, while ancient glacial deposits are known in the present tropical zone. Presumably, there have been, throughout geologic history, climatic rhythms—times in which conditions were mild and equable have alternated with periods of sharply zoned climates. There are, however, other possible explanations. Some have suggested a wandering of the poles and consequent readjustments of climatic bands, others an actual movement of continental areas.

The vertebrates themselves offer evidence as to the climates in which they lived. Living "cold-blooded" reptiles and amphibians cannot exist in arctic or subarctic regions, and most of the extinct ones may have had similar limitations. But this type of reasoning must not be carried too far. Elephants and rhinoceroses today are tropical animals; but we know that, in the Pleistocene, hairy types closely related to living forms in both groups existed near the glacial front. The evidence of plant and invertebrate life is important in determining climatic conditions. Plant types now characteristic of the tropics once grew in Greenland. It is probable that this indicates a former warm climate there; but it is possible that plant habits have changed. The sediments themselves commonly suggest the nature of the climate under which they were formed. For example, striated rock surfaces and deposits similar to those made by recent glaciers are indicative of ancient ice ages. But the evidence of sediments is not always beyond doubt. Red beds, for example, were long thought to indicate aridity; but red deposits are now being laid down at the mouth of the Amazon and in other warm regions of abundant rainfall.

Migrations.—No matter how potentially successful a newly evolved form may be, obstacles are often present which prevent its invasion of regions in which it might flourish. The greater part of the world has always been covered by seas, and migration is comparatively easy for marine forms. Even here, however, barriers may exist, due, for example, to differences in water temperature or salinity. For terrestrial forms there are numerous types of barriers. Forests, deserts, and mountains, as well as temperature differences, are often effective bars to migration. The greatest obstacle, however, is the lack of a land connection, the interposition of a broad body of water between continental areas. Many oceanic islands have no native land vertebrates of any sort; no terrestrial mammal has ever reached New Zealand.

Viewed on the ordinary Mercator map, intercontinental migration appears a complicated process. On a north polar projection, however, the situation is much simplified. Europe and Asia form a unit, and North America is separated from them only by a narrow strait across which dry land is believed to have stretched at many times. From this northern land mass depend three great southern peninsulas, South America, Africa, and Australia. The first two are connected with the north by narrow isthmuses believed to have been under water in earlier times, while Australia is separated by an island-studded region which may once have been dry land. Many of the facts of vertebrate distribution in past and present times are readily explained by a make or break of these four connections.

Land bridges have often been built in the minds of scientists to account for certain facts of distribution. Some of these structures are quite fanciful, made in an attempt to explain the real or supposed resemblances between one or two animal types in two disconnected regions but disregarding the divergences between the two regions in other animal groups. Others, however, deserve more serious consideration. This is especially true of bridges advocated between the three southern continents. The presence of carnivorous marsupials in Australia and in the South American Tertiary has suggested the possibility of a former land connection between these two areas. South America and Africa show resemblances not only in some mammalian types but also in some groups of fresh-water teleostean fishes and in the presence of related lungfish genera, and a connection between them in the early Tertiary has been strongly advocated. Elsewhere it has been pointed out that many of these facts may be accounted for by the former presence of the common types or their ancestors in northern areas from which these continents might have been reached without any major change in land areas. One must not "erect" a bridge for the convenience of one group of animals without taking into account its effect upon other elements of the fauna. For example, hystricoid rodents with relatives in Africa appear suddenly in South America in the Oligocene. A transatlantic land bridge would afford easy access for the rodents and an easy solution for the problem concerning them. But in both continents there were numerous other animals that one would think equally capable of crossing such a bridge. There is, however, no evidence that they did cross. Land bridges that transmit but one type of animal, and in but one direction, may have existed; but their existence is highly improbable.

Such bridges, however, may have been somewhat selective in their nature in many cases. The present "bridge" between the two Americas has allowed the passage of many animal types. Among the ungulates, deer, peccaries, tapir, and camelids have made successful southern migrations, but the plains-loving bison never penetrated beyond Honduras into this region of tropical jungles and mountains. The Behring Straits connection between Asia and Alaska was a well-traveled highway of migration in the Pleistocene. But warmth-loving animals, such as most of the antelopes, the giraffes, and hippopotami, were unable to cross.

"Island hopping" is a partial solution for some problems of migration. Asia and Australia have not been in direct contact, it seems certain, at any time during the Cenozoic. Between them, however, stretch the East Indies, separated by short gaps, certain of which may have been, at times, dry land. Scattered down the island chain one finds a decreasing percentage of placental mammals of Asiatic origin. Certain rat types have made the whole series of "hops" to Australia; a few marsupials have worked part of the reverse journey.

It seems certain that land animals do at times cross considerable bodies of water where land connections are utterly lacking. The West Indies and Madagascar, for example, have sparse mammalian faunas which are composed of a few odds-and-ends of the numerous mammal groups found on the neighboring continental areas. Obviously, these forms have reached their island homes by some chance type of oversea transport. Floating masses of vegetation, such as are sometimes found off the mouths of the Amazon, may be one means of effecting this type of migration. Even the case of the entry of the hystricoids into South America may be a case of this sort. The South Atlantic is broad, and the chances of a crossing very poor; but Tertiary time was long, and one successful crossing might populate a continent.

A majority of geologists believe that the existing continents have preserved their identities and locations through a vast period of time, and this has been tacitly assumed above. Many workers, however, incline to a belief in floating continents; it is suggested that the land surface of the earth once constituted a single mass, from which America has broken away westward and Australia spread to the east. Most of the continental connections suggested by this theory are quite unnecessary for the explanation of vertebrate distribution, and some of the Cenozoic continental relations assumed are at variance with the facts of vertebrate history. But, in general, the hypothesis is neither strongly supported nor disproved by vertebrate evidence, and its truth or falsity must be decided from other lines of evidence.

CAMBRIAN

During the Cambrian, earliest of the Paleozoic periods, almost every major type of invertebrate life makes its appearance, and many groups have already become so highly organized and diversified that we may be sure that they have already been in existence for a long period of time. But vertebrates appear to be absent from the record. This might perhaps be accounted for by the fact that the probable ancestors were soft-bodied forms which we should not expect to find fossilized under ordinary conditions. But even in the case of a remarkable Middle Cambrian deposit in British Columbia in which the shales have preserved very delicate impressions of soft-bodied invertebrate types such as jellyfishes, no chordates of any sort have been recognized. Either vertebrate ancestors were extremely rare or else were absent from the salt waters in which all well-known Cambrian deposits were laid down.

ORDOVICIAN

Ordovician sediments are likewise predominantly marine in origin. Invertebrates are abundant and diversified, but vertebrates have been reported in but one formation, and these are fragmentary remains not giving us any idea of the appearance or anatomy of these forms. In the early Upper Ordovician Harding Sandstone of Colorado and other western states are scraps of material which in microscopic structure are seen to be pieces of the dermal armor of vertebrates, presumably ostracoderms. The sediments are considered estuarine in nature. A reasonable interpretation is that the vertebrate scraps are those of stream-living types whose remains were carried down to river mouths. This is but one of many lines of evidence strongly suggesting that the Lower Paleozoic vertebrates developed in inland waters. Their almost utter absence from the fossil record of the first half of the Paleozoic may be correlated with the fact that almost no continental sediments of such high antiquity are known today.

SILURIAN

For most of the Silurian the sedimentary record is again one of marine areas and abundant marine life, with little or no trace of vertebrates. In the late Silurian, however, began the Caledonian Revolution, a time of earth disturbances and of the building in Europe of great mountains, of which the Scottish Highlands and the Scandinavian ranges are remnants. The erosion of materials from these mountains resulted in greatly increased continental deposits in northern Europe from Great Britain to Spitzbergen and Russia. In these beds are found the oldest adequately known vertebrate types.

The earlier Upper Silurian deposits of Europe, grouped as the Ludlow, tended to change in type from marine to estuarine or even continental sediments. Typical marine invertebrates become rarer near the top of the series, and there remain only such types as the eurypterids, which may have been fresh-water forms. With this progressive change, vertebrates make their appearance and become increasingly numerous. In western England the Ludlow bone bed, a layer scarcely a foot thick but of wide extent, derives its name from the fact that it is full of tiny vertebrate plates and spines. The latest Silurian of Europe is termed the Downtonian. It consists in great measure of red sediments, "Passage Beds," difficult to distinguish from the overlying Old Red Sandstone and so similar to that series that some writers have advocated placing these beds in the Devonian. Numerous vertebrate finds have been made in these "Passage Beds" in western England, southern Scotland, southern Norway, Spitzbergen, and Podolia. In general, the conditions are of a nature suggestive of fresh-water origins. An exception, however, is the important locality of Oesel in the Baltic, where vertebrate-bearing layers occur in a limestone series, interdigitated with others carrying a marine fauna; conditions here have been interpreted as estuarine. In the America Silurian, vertebrate localities are few in number, and finds are rare; they are for the most part in sediments comparable to those of the Downtonian. There are no records of Silurian vertebrates in any other region.

The only well-preserved vertebrates are, as might be expected, agnathous types. All major groups of ostracoderms are present and are highly developed and diversified. They appear to have been then at the peak of their career and to have had behind them a long history, of which, because of lack of earlier continental sediments, we know almost nothing. There are abundant cephalaspid types, such as *Tremataspis* and *Hemicyclaspis*, and numerous primitive pteraspids (*Poraspis*, *Anglaspis*, *Cyathaspis*, etc.). Nearly all the known anaspids, such as *Birkenia* and *Pharyngolepis* are from the Downtonian, as are most of the remains of the problematical coelolepids, as *Thelodus* and *Lanarkia*.

No skeletons of jawed vertebrates have as yet been discovered in the Silurian. But such was the variety of these forms in the overlying Lower Devonian that it is certain that they were undergoing development in the Silurian. Proof of this is afforded by the fact that the late Silurian bone beds are filled with spines and plates which probably belong in some measure to forerunners of the acanthodians and arthrodires of the early Devonian. The fragmentary nature of these remains suggests that they had been washed down from areas farther inland, in which the evolution of jawed fishes was in progress—the higher reaches of streams in the uplands formed as a result of the Caledonian mountain-building. But it is almost beyond hope that these ancestral forms will ever be found as fossils, since such highland areas are regions of erosion rather than of deposition.

DEVONIAN

Although amphibians had evolved by the end of the Devonian, this period is often, and reasonably, called the "Age of Fishes." The short list of Silurian vertebrate localities was confined essentially to fresh-water deposits of Europe and eastern North America. In the Devonian our perspective widens. As will be seen, new continental areas are added to the list before the close of the period; further, some of the lower fish groups rapidly spread into salt-water environments, and hence marine formations of the later Devonian frequently include vertebrate remains.

Devonian localities.—The classic localities for Devonian fresh-water fishes are those of the Old Red Sandstone of Great Britain, particularly

TABLE 2

PALEOZOIC VERTEBRATE LOCALITIES

	European Stages	Europe	North America	Other Continents
PERMIAN	Thuringian (Tartarian)	Sarma fm., N. Dvina R.-"Zone IV" (Russia); Cutties Hillock (Scotland); Zechstein of Germany		*Cisticephalus* and *Endothiodon* zones of Beaufort series (S. Af.); Ruhuhu, Tanga (E.Af.); Chiweta beds (Nyassaland); Mangwa (Rhodesia); Bijori beds (India); Upper Newcastle Coal Measures (Aus.)
	Saxonian (Kazanian)	Kupferschiefer (Ger.); Magnesian ls. and Marl slate of Durham (Eng.); "Zones I-III" of E. and N. Russia	Coconino, Kaibab (Ariz.)	*Tapinocephalus* zone of Beaufort series (S. Af.)
	Autunian (Artinskian, Kungurian)	Rotliegende at Niederhässlich, Lebach (Ger.); Braunau (Bohemia); Autun (Fr.), etc.; Warwickshire (Eng.); southern Norway	Wichita and Clear Fork beds of Texas and other red beds in N.M. (Abo), Ariz., Okla., Kans., W.Va., etc.; Phosphoria fm. (Wyo.) *M*;* E. Greenland *M*	Ecca (S.Af.) (barren); Dwyka (S. Af.); Itarare (Brazil); Mhum Mu (Kashmir)
PENNSYLVANIAN	Stephanian (Uralian)	Nýřany, Kounová (Bohemia); Commentry (Fr.)	Conemaugh, Monongahela, L. Dunkard (Pa., W. Va., Ohio); Danville (Ill.)	
	Westphalian (U. Muscovian)	English coal fields of Newsham, Yorkshire, Staffordshire, etc.; Kilkenny (Ire.)	Alleghany of Linton (Ohio); Mazon Cr. (Ill.); Joggins (N.S.)	
	Namurian (Lanarkian, L. Muscovian)	Scottish coal fields		
MISSISSIPPIAN	Dinantian-Visean, Tournaisian	Edinburgh coal field—Loanhead, Gilmerton, Airdrie, etc. (Scot.); Calciferous ss. and Cementstones of S. Scotland—Burdiehouse, Wardie, Eskdale, etc.; Limestones near Bristol (Eng.), Armagh (Ire.) *M*	Mauch Chunk at Hinton (W.Va.); Albert Mines (N.B.) St. Louis, Keokuk, Burlington ls. (Ia., Mo., Ill.) *M*	

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* *M* = Marine.

TABLE 2—*Continued*

	European Stages	Europe	North America	Other Continents
DEVONIAN	Famennian, Frasnian (Chautauquan, Senecan of N.A.)	U. "Old Red" of Scotland, Shetland, W. Eng.; Baltic States; Russia; Rhineland (Wildungen, etc.) *M;* Boulogne region (Fr.) *M*	"Catskill" of N.Y. and Pa.; Scaumenac Bay (Que.); Colo., Ariz.; Ellesmere Land; E. Greenland; Cleveland Shale (Ohio) *M;* "Chemung" of N.Y. and Pa. *M;* Cedar Valley (Ia.) *M;* Milwaukee (Wis.) *M;* Hamilton of N.Y., Ont. *M*	Antarctica; Victoria, N.S. Wales (Aus.); central Asia
	Givetian, Eifelian (Erian, Ulsterian of N.A.)	M. "Old Red" of N. Scotland, Orkneys, Shetlands; Baltic States; Wijhe Bay series (Spitzbergen); Rhineland *M*	Ellesmere Land; E. Greenland; Onondagan ls. of N.Y., Ont., Ind., *M;* Columbus and Delaware lss. of Ohio, *M*	N.S. Wales (Aus.)
	Emsian, Siegenian or Gedinnian, Dittonian (Oriskanian, Helderbergian of N.A.)	Podolia (Ukraine); L. "Old Red" of S. Scotland and W. Eng.; Wood Bay and Grey Hoek series of Spitzbergen; Rhineland *M* (in part)	Campbellton (N.B.); Beartooth Butte (Wyo.)	
SILURIAN	Downtonian (Cayugan of N.A. in part)	Red Downtonian "Passage Beds" (Scotland); Temeside shales, Downton ss. (W. Eng.); Podolia (Ukraine); Oesel (Esthonia); Gottland (Sweden); S. Norway; Red Bay (Spitzbergen)		
	Ludlovian (Cayugan of N.A. in part)	Lanarkshire (Scot.); Whitcliffe Flags, Ludlow bone bed (W. Eng.)	Salina (Perry Co., Pa.)	
	Salopian (Wenlockian, Niagaran of N.A.)		Rose Hill fm. (Pa.); Neperis Hills (N.B.)	
	Valentian (Medinan of N.A.)		Shawangunk (N.Y.)	

Scotland. These continental deposits embrace nearly the whole extent of the Devonian and are divided into lower, middle, and upper portions. The Lower Old Red is, we have noted, essentially continuous with the underlying Downtonian; it is well represented in southern Scotland and western England. The Middle Old Red, richly fossiliferous, is found in large areas of northern Scotland—the Moray Firth region, Caithness, the Orkneys, and even the Shetland Islands. The Upper Old Red is, in contrast, more limited in extent and confined to a number of small areas in England and southern and central Scotland.

Sediments comparable in nature and in faunas are found in many other regions. Lower Old Red equivalents are present in Podolia, in Spitzbergen, and in America at Campbellton, New Brunswick, and Beartooth Butte in Wyoming. Sediments of the type of the Middle and Upper Old Red are still more widespread—Spitzbergen, eastern Greenland, Ellesmere Land, the Baltic States, western and northern Russia, and Australia. Deposits equivalent to Upper Old Red are common in continental North America. Scaumenac Bay in eastern Canada is a famous locality of this age, and in New York State there is a great series of Upper Devonian red beds to which the term "Catskill" is often (but loosely) applied. Fish faunas of this age and type are further found in northern and central Asia and even Antarctica and hence extend nearly from pole to pole. It may be noted that these "Old Red" faunas appear to be remarkably uniform in nature; at any given horizon the same genera may be found in areas far removed from one another.

During the course of the Devonian, marine localities become increasingly important for the vertebrate record. The mountains of the middle Rhine in Germany show a series of sediments of this type. In the late Lower Devonian there are here several beds with vertebrate remains, interlarded between purely marine layers and probably brackish in nature. In the Middle and Upper Devonian there are numerous vertebrate localities in western Germany which appear to be typically marine; Wildungen, with an abundant Upper Devonian fish fauna, is the most famous.

Middle and Upper Devonian deposits similarly marine in nature contain vertebrates in a number of other regions, particularly North America. In the Middle Devonian there are plentiful fish remains in the Columbus and Delaware Limestones of Ohio and their equivalents in other states. In the Upper Devonian, the "Chemung" deposits in western New York and Pennsylvania contain marine vertebrates. The black Cleveland shales of Ohio, which lie close to the Devonian-Mississippian boundary, are notable for the variety of their vertebrate remains and for the delicate preservation of some of the sharks found in them.

Lower Devonian fishes.—The fish fauna of the Lower Devonian differs markedly from that of later portions of the period and is in great measure simply a continuation of that seen in the late Silurian. Ostracoderms are still fairly abundant, although not so numerous or so varied as earlier. There are a number of genera of the *Cephalaspis* and *Pteraspis* groups; anaspids and coelolepids, however, are relatively rare in the Devonian.

Jawed fishes are now added in abundance to the faunal assemblage. There are, however, no Chondrichthyes identified and, except for one rare forerunner of the crossopterygians (*Porolepis*), no higher bony fishes. The early Devonian gnathostomes are predominantly placoderms. They are already diversified, and two groups are plentifully present. Acanthodian "spiny sharks" are now, in their first definite appearance, at their height in variety and abundance in such genera as *Parexus*, *Climatius*, etc. A second common placoderm group is that of *Arctolepis* and other primitive arthrodires with enormous pectoral spines.

In general, there is little reason to believe this fauna to have been other than a fresh-water one. In the Rhineland Lower Devonian, however, we find an assemblage of fishes suggestive of a change to, or at least toward, a marine life. Some of the normal "Old Red" elements are present, but, in addition, there are the curious armored but sharklike stegoselachians, *Gemuendina* and *Stensioella;* an odd, arthrodire-like type, *Lunaspis;* and an abnormal heterostracan, *Drepanaspis*. These forms seem to be representative, in part, of the ancestors of the marine forms of the later Devonian.

Later Devonian fresh-water fishes.—Although deposits of "Old Red" type continued without interruption into middle and late Devonian times, their fauna changed greatly. Except for a few rare cephalaspids and anaspids, the once abundant ostracoderms have disappeared. The placoderm assemblage has changed in character. Acanthodians persisted through the Devonian—indeed, into the Permian—but are then and thereafter relatively rare types. Arthrodires are present in these continental sediments but are not abundant. *Coccosteus* is an "orthodox" arthrodire of advanced type; *Homostius*, *Heterostius*, and *Phyllolepis* are depressed forms, perhaps indicative of brackish-water conditions; ptyctodonts, such as *Rhamphodopsis*, are rare in continental deposits. *Palaeospondylus*, a tiny form perhaps belonging to the placoderms, is known from but a single quarry in Scotland but is very abundant there.

New additions to the placoderm group are the antiarch genera, such as *Asterolepis*, *Pterichthyodes*, and *Bothriolepis*, which were among the most common fishes of middle and late Devonian times.

The sharp decline among these lower fish groups (antiarchs excepted) is apparently due to the sudden appearance, in great abundance and variety, of the Osteichthyes, the higher bony fishes. In the Middle and Upper "Old Red" and its equivalents, there are numerous rhipidistian crossopterygians (such as *Osteolepis* and *Eusthenopteron*) which were the dominant predaceous forms of their times, and rare primitive coelacanths. Dipnoans flourished in such genera as *Dipterus* and *Scaumenacia*, similar in externals to their crossopterygian cousins but already specialized in skull and dental structure. Present, too, were primitive actinopterygians—the palaeoniscoids *Cheirolepis*, *Stegotrachelus*, and *Rhadinichthys*—but, in contrast to their later abundance, they were rare until late in the period.

This marked change in the vertebrate assemblage—this sudden appearance of the Osteichthyes—is an important milestone in vertebrate history. Only a few fragments of a single rare form were present to represent this entire class in the Lower Devonian, and yet, at the time of their Middle Devonian incursion, the various types were already quite distinct, with implications of a long antecedent history. Where their evolution took place—in upper river reaches or in some unknown continental area—is a major question to which we have no ready answer.

Marine life.—The seas of the later Devonian witnessed an evolutionary development among fishes quite different in many respects from that seen in inland waters. The Agnatha are rare, although the heterostracan *Psammosteus* and its relatives persisted in presumed estuarine conditions, and although we must, further, assume the survival of degenerate agnathous forms ancestral to the modern cyclostomes. Placoderm history in the seas was a different story from that of streams. The presence of marine acanthodians in the late Devonian is suggested by numerous spines of appropriate character, and the stegoselachians persisted in later marine deposits. *Lunaspis* of the Lower Devonian was antecedent to *Macropetalichthys* and related forms, widespread in mid-Devonian limestones. The antiarchs appear to have, in general, kept to fresh waters. Arthrodires, however, flourished greatly in the Devonian seas. In the Upper Devonian, particularly in the Rhineland and the Cleveland shales, are found a great number of advanced arthrodires, varied in structure and varied in size from forms of modest proportions to giants like *Dinichthys*.

Parallel to the deployment of the Osteichthyes in inland waters was the rise of the Chondrichthyes in the seas. The sharklike fishes are unknown in the Lower Devonian, although the stegoselachians suggest the nature of their evolution, and even in the Middle Devonian we can identify them only from a few teeth of the primitive *Cladodus* type. By the end of the period, however, primitive sharks—*Cladoselache* and *Ctenacanthus*—were highly developed; their structure is well shown by specimens in the Cleveland shale, which have preserved in remarkable fashion even such soft and microscopic structures as muscle-fiber striations. In late Devonian deposits we further find teeth showing the appearance of the bradyodont mollusk-eaters and possibly the pleuracanths.

Fish evolution in the Devonian.—The close of the Devonian witnessed the decline or disappearance of many important fish groups. The ostracoderms were already reduced in numbers early in the period and did not survive its close. Antiarchs and arthrodires, although numerous in the Upper Devonian, disappeared before the opening of the Carboniferous. In the space of a single period, almost every fish type present in the Lower Devonian was wiped out except for a few acanthodians.

The more important events in Devonian fish history include (1) the decline and fall of the ostracoderms; (2) the rise and decline of the acanthodians; (3) the rise and disappearance of the arthrodires; (4) the appearance in the middle Old Red of the flourishing antiarchs and their extinction at the close of the period; (5) the rise of sharklike forms in the late Devonian; and (6) the sudden appearance in the middle Old Red Sandstone of the bony fishes.

For completeness, this body of knowledge leaves much to be desired. A chronological treatment tends only to throw into stronger relief the fact that we know almost nothing of the origin or real relationships of most of the early fish groups.

Amphibians.—It was noted in earlier chapters that the Devonian was probably a time of marked seasonal droughts; much of the success of the bony fishes (and perhaps the antiarchs) may have been due to their possession of lungs and other drought-resisting adaptations. The amphibians appear to have been, in their initial period, merely another fish group which had developed terrestrial locomotion as a further device helpful under Devonian conditions of life, and their early development from the crossopterygians occurred in that period. The first stages in their history are, however, poorly known; we possess only a skull roof (*Elpistostege*) from the Upper Devonian of Scaumenac Bay, which is that of a very fishlike amphibian or very amphibianlike fish, and, from a Greenland formation close to the Devonian-Carboniferous border, several skulls of the primitive ichthyostegid amphibians.

CARBONIFEROUS

The time covered by the deposits frequently grouped as the Carboniferous Period is very great. In North America a division into two periods—Mississippian and Pennsylvanian—is now customary, for there is generally a decided contrast between a lower division in which marine limestones predominate and an upper one characterized by coal seams and shallow-water deposits. Since the fish faunas which still constitute the bulk of vertebrate remains are not sharply contrasted, we shall here consider the Carboniferous faunas as a unit.

Vertebrate localities.—The Lower Carboniferous, or Mississippian, is predominantly marine and is represented, for the most part, by thick series of limestones. These frequently contain rich invertebrate faunas; less frequently they contain the remains of marine fishes, usually in the form of isolated spines or teeth. Formations and localities of this sort include the St. Louis, Burlington, Keokuk, and other limestones of the Mississippi Valley; a rich horizon in the Carboniferous limestone series near Bristol, England; a similar formation at Armagh in northern Ireland; and numerous other limestone localities in western and central Europe and Russia.

Continental deposits are, on the other hand, rare. In North America there are few localities of this sort; exceptional are those at Albert Mines, New Brunswick, where large numbers of a few species of fresh-water fishes are present in oil shales and at Hinton, West Virginia, where a few fishes and amphibians have been recovered from a late Mississippian shale. In other continents there is likewise an almost complete lack of Mississippian fossils of continental origin. Scotland forms the sole exception. In the southern part of that country the Lower Carboniferous is highly developed. Some limestones are present, but materials of a more continental type are prominent calciferous sandstones, oil shales, and even coal seams. At various localities, often seemingly estuarine in nature, there are rich fish faunas and, in addition, near the Firth of Forth, occasional finds of amphibians.

Pennsylvanian fossil deposits are, in contrast to those of the Mississippian, predominantly continental in type. This was the time at which the most important coal seams of Europe and North America were formed; and numerous inhabitants of the coal-swamp pools have been preserved in the shales, ironstones, and impure cannels associated with the coals. In Europe the typical Coal Measures are included in the Westphalian floral zone. Although coals of this age are abundant on the Continent, Westphalian fossil finds are almost entirely confined to the British Isles, where Newsham near Newcastle and Kilkenny in Ireland are important localities. In the late Pennsylvanian appears the Stephanian flora, transitional to that of the Permian. The coals of this horizon are well represented on the Continent, and Stephanian vertebrates are richly represented at Nýřany (Nürschan) and Kounová in Bohemia.

In America the earliest Pennsylvanian formations—those of the Pottsville—are, so far as is known, barren. In the somewhat later formations, equivalent to the Westphalian of Europe, there are several rich deposits, including a pocket of fossiliferous cannel coal at Linton, Ohio; nodules containing vertebrates, as well as plants, in the coal shales at Mazon Creek, Illinois; and material filling the hollow stumps of coal-swamp trees at the Joggins, Nova Scotia. Other scattered North American localities are of late Pennsylvanian age (Stephanian). In some areas and horizons typical Coal Measures conditions persist; in others there is a transition to red sediments, which continue without break into the Permian.

Despite the predominance of discoveries of continental forms of life, marine vertebrates are not uncommon finds in the Pennsylvanian. Some are present in typical marine beds. More important, however, is the fact that coal deposition was not a continuous process but a cyclical one, and layers of marine origin containing teeth and spines of sea dwellers are frequently present between successive coal horizons.

Fresh-water fishes.—The character of Carboniferous fish life in inland waters was markedly different from that of the Devonian. Of lower fish groups, the ostracoderms were extinct; gone, too, were the antiarchs so numerous in the late Devonian. Acanthodians persisted in small numbers, and, of the sharklike fishes, the pleuracanths were common in many localities. All other fresh-water forms were members of the Osteichthyes. But, although the groups represented were the same as in the later Devonian—crossopterygians, lungfish, and palaeoniscoids—their relative abundance had changed greatly in character. In the Devonian the two choanate groups were dominant, the ray-fins rare. In the Carboniferous, perhaps in correlation with changed environmental conditions, the proportions were reversed. *Megalichthys* and a few other crossopterygians, including fresh-water coelacanths, survived in reduced numbers; the dipnoans, as *Sagenodus* and *Ctenodus*, were a modest group. They were vastly outnumbered by a host of palaeoniscoids, which appear to have swarmed in every Carboniferous pool and river. About two-score genera have been described; some were still rather primitive in nature, others specialized or advanced in various degree.

Marine fishes.—In the sea as on land, the archaic fish groups were reduced in numbers. There are no ostracoderms; of the placoderms, fin spines suggest the survival of large acanthodians, but the arthrodires are absent. Nor was there any notable tendency, as yet, for a marine invasion by the higher bony fishes.

The Chondrichthyes, however, developed greatly in the seas of this age. Seldom are entire specimens preserved, but abundant teeth and spines testify to the number and variety of sharks and sharklike fishes in these oceans. Most abundant were the bradyodonts, mollusk-eating forms which appear to have been depressed bottom dwellers analogous to the later skates and rays; there are four families and a variety of genera of bradyodonts, which had already reached the peak of their development in the Mississippian. These fishes were presumably a major prey of the predaceous shark types which were also common inhabitants of the Carboniferous seas. Of these sharks, some continue to represent the primitive *Cladoselache-Ctenacanthus* group, which had appeared in the later Devonian; others, however, appear to have become more "modernized" in fin structure and belong to the hybodont family, destined to continue into the Mesozoic.

Amphibians.—The Carboniferous is the time of greatest development of the amphibians. Once evolved, with the possibilities of amphibious, if not terrestrial, life before them, they had spread into a host of types varying greatly both in structural features and in adaptations. Of the two major groups present, the labyrinthodonts are the better known, partly because of their tendency to grow to large size. The Devonian ichthyostegids persisted but are relatively rare finds. Embolomeres were common inhabitants of the coal-swamp lagoons; many, such as *Eogyrinus*, were elongate and slender fish-eaters and persistent water dwellers. Toward the close of the Carboniferous appear *Diplovertebron* and other forms approaching the reptiles in many structural features. The *Loxomma* group, apparently very common for much of this time, may be an offshoot of the Rhachitomi; more representative, although primitive, members of this group, such as *Dendrerpeton*, appear in the Pennsylvanian. Presumably of labyrinthodont derivation were *Amphibamus* and *Miobatrachus*, which appear to show an initial stage in the evolution of the frogs.

Less conspicuous because of smaller size but more abundant and varied were the lepospondyls. They appear in early Mississippian horizons and had already reached and passed their time of major development by the close of the Carboniferous. There were snakelike aistopods, *Dolichosoma* and *Ophiderpeton;* numerous nectridians, including "horned" forms such as *Keraterpeton*, and the elongate *Urocordylus;* and a host of varied microsaurs, such as *Microbrachis*, *Coccytinus*, and *Hylonomus*.

Reptiles.—The development of reptiles, primarily characterized by their improved reproductive processes, took place during the Carboniferous. Unfortunately, our record of their early history is poor, owing, one may believe, to the fact that most Coal Measures localities are deposits of a nature which tends to include pool dwellers rather than inhabitants of the dry land. Late Pennsylvanian records show that the reptiles had at that time become as diversified as in the Permian; for we find not only specialized cotylosaurs of the diadectid type but pelycosaurs—even the peculiar, long-spined *Edaphosaurus*. In the earlier, Westphalian, Coal Measures there are a few obscure specimens which may be those of early cotylosaurs, but their nature is none too clear.

PERMIAN

Sediments.—Toward the close of the Carboniferous a gradual change in sediments occurred in many portions of western Europe and North America. Coal seams and intervening marine beds gradually gave place to terrestrial deposits prevailingly red in color, their materials derived from the great mountain masses then being formed, such as the ancestral Alps in Europe and the ancestral Rockies and the earliest Appalachians in North America. This change in sediments was gradual, and only arbitrary lines of division can be made between the Upper Carboniferous and the Permian red beds; correspondingly, we find that the vertebrate life of the late Pennsylvanian is almost indistinguishable from that of the early Permian. In North America an abundant Permo-Carboniferous land fauna appeared in late Pennsylvanian times and persisted well into the Lower Permian. Red beds containing these forms are found in regions as far apart as New Mexico and Prince Edward Island but are best developed as the Wichita and Clear Fork groups in northwestern Texas. The many specimens collected from the latter region give us our best picture of the world's early Permian life.

In Europe the lower Permian—the Rotliegende—is a series comparable in nature to the American red beds; the known fauna, however, is more restricted, presumably because of fewer exposures. A few specimens have been recovered from beds of this age in England, France, and Czechoslovakia; the most famous locality is that at the Plauen'schen Grunde (Niederhässlich) near Dresden, where slabs containing remains of numerous small amphibians and reptiles have been obtained.

These fossiliferous red-bed deposits cover but the earliest portion of the Permian. In America further red-bed deposition continued through much of the period, but these levels have not yielded the slightest trace of bone. In western Europe the Rotliegende is followed by the Kupferschiefer and the marine phases of the Zechstein, with a sparse fish fauna and almost no tetrapods. For land vertebrates of the Middle and Upper Permian we must turn to other areas—South Africa and Russia.

In Africa pre-Permian vertebrates are unknown; there are no fossiliferous early Paleozoic sediments of any sort, and those of the Devonian and Carboniferous are almost exclusively marine. At the close of the Carboniferous, however, there began the formation of the continental deposits of the Karroo system, some thirty thousand feet thick, which cover much of the Union of South Africa and have outliers in central and eastern Africa and Madagascar. At the base is the Dwyka series, late Pennsylvanian or earliest Permian in age, containing glacial beds and with a sparse vertebrate fauna. Following this are some six thousand feet of the Ecca series, a barren equivalent of the lower Permian red beds of Europe and North America. The Beaufort beds begin with the Middle Permian and continue without marked break, lithologically or faunally, into the Triassic. Their exposures cover a great area centering in the Karroo desert of northern Cape Colony and have a rich tetrapod fauna. Several zones, named after index reptiles (*Tapinocephalus*, *Endothiodon*, *Cisticephalus*) are distinguishable in the Permian portion of the series.

Few fossiliferous continental formations of Permian age are as yet reported from Asia or Australia; and, although Brazil has sediments of Karroo type, the Permian beds are unfossiliferous except for a Dwyka equivalent. In eastern and northern Russia, however, is found a series of continental deposits which corresponds closely to the Permian portion of the Karroo system. Although known for a century, serious exploration of these beds has only recently begun; they promise to yield a fauna as interesting as that of South Africa. A single "pocket" near Elgin, Scotland, appears to be an outlying equivalent of the latest Russian Permian.

Marine Permian formations are abundant, but most are barren of vertebrates. A few fishes only have been found in early Permian limestones in scattered areas of North America (Texas, Nebraska, Wyoming, East Greenland), Russia, southern Asia, and western Australia. In the later Permian the Kupferschiefer deposits of Germany appear to have been laid down in brackish lagoons.

Fishes.—As our discussion of localities suggests, marine fish life is almost unknown in the Permian. In the earliest horizons there are a few representatives of common Carboniferous chondrichthyan groups—the last cladodont sharks, bradyodonts, and hybodonts; there is little evidence of any salt-water bony fish in the early Permian. *Menaspis* and *Janassa* in the Kupferschiefer are the last of the once abundant bradyodonts, and there were a few surviving hybodonts. The old vertebrate fauna of the oceans appears to have been almost entirely wiped out at the close of the Paleozoic, although it is certain that some hybodonts and bradyodont descendants must have survived to give rise to the sharks and chimaeras of later times. The first marine radiation of the vertebrates was at an end.

In fresh waters, *Acanthodes* survived into the Lower Permian as the last of the once important placoderms. *Pleuracanthus* was a common early Permian fresh-water shark but is unknown in later times except in Australia, where the group appears to have persisted into the Triassic. The Lower Permian also sees the end of rhipidistian crossopterygians; *Ectosteorhachis* in America is the last survivor of this phylogenetically important group. Coelacanths, however, persisted in fresh waters. Lungfishes, particularly *Sagenodus*, were common at the beginning of the period but are unrecorded later.

The dominant types are palaeoniscoids. Relatively few genera are known, but they appear to have been varied in nature and included such unusual and progressive types as *Dorypterus*. A single holostean in the late Permian marks the beginning of the change in actinopterygian faunas to be witnessed in the Triassic. The Kupferschiefer deposits contain actinopterygians which may have been able to withstand brackish, if not strongly saline, waters and may represent the beginning of the first major invasion of the seas by the ray-finned fishes.

Amphibians.—There is no marked break between the late Pennsylvanian and early Permian in amphibian faunas; the red beds exhibit a final phase in Carboniferous amphibian history. There are surviving embolomeres and seymouriamorphans, such as *Archeria* (“*Cricotus*”) and *Seymouria*. The rhachitomes were already present in the Carboniferous but reached the peak of their development in the Lower Permian. *Eryops* was the common and characteristic large form in the American red beds; *Actinodon* and related types were comparable European genera. In addition, there were a score or more of rhachitomes of varied character—the dissorophids, armored and with exaggerated otic notches; long-snouted aquatic types such as *Archegosaurus* and *Chenoprosopus;* the flat-headed *Trimerorhachis*. Lepospondyls were reduced greatly in numbers, but there were a few survivors, such as *Diplocaulus*, *Lysorophus*, and the gymnarthrids.

In the later Permian, amphibian life was much reduced. The degenerate genus *Kotlassia* represented the seymouriamorphs in the late Permian, but the embolomeres have disappeared. Gone, too, are the lepospondyls (with one possible exception). The Rhachitomi alone persisted in moderate numbers, in such forms as *Rhinesuchus*, which, with flatter heads and broadly opened palatal vacuities, were entering on a "neorhachitomous" condition foreshadowing the stereospondyls of the Triassic.

Cotylosaurs.—Reptile origins took place in the Carboniferous, but it is only with the development of more terrestrial conditions in the red beds that we can gain a comprehensive picture of early reptilian life. The "stem reptiles" were an important factor in the land fauna of the early Permian. Some types, as *Limnoscelis*, appear to be very primitive; most cotylosaurs, however, are advanced or specialized in nature, showing that their point of common divergence must have been far back in the Pennsylvanian. *Captorhinus* and *Labidosaurus* are examples of the advanced American captorhinomorphs of the early Permian. The commonest of early cotylosaurs, however, are those of the *Diadectes* type, presumed herbivores with highly specialized cheek teeth.

In the later Permian, captorhinomorphs are extinct, or nearly so, and the remaining forms are herbivorous diadectomorphs. In the Russian Middle Permian are two types of procolophonids—small cotylosaurs which were destined to survive and flourish in the Triassic. More abundant in the later Permian, however, were the pareiasaurs. These ungainly-looking creatures are the commonest of finds in the Middle Permian of South Africa. Their remains are frequently found as if in the position in which they had become bogged down in the swamps where they found their food and met their death. In the Upper Permian of South Africa, pareiasaurs are relatively rare; they were, however, widespread at this time, for there are Upper Permian pareiasaurs in Russia and even in Scotland.

Pelycosaurs.—It is of interest that the most prominent of early reptilian orders is not a primitive group or one which led to later typical reptiles but one destined, after many changes and vicissitudes, to give rise to the mammals. Pelycosaurs had arisen in the later Carboniferous as an early offshoot from the stem reptiles and still retained many primitive features. They were highly diversified in the red beds. Some, like *Ophiacodon*, were long-snouted, semiaquatic fish-eaters. *Edaphosaurus*, with long spines and crossbars, and *Casea* were representative of a side line of herbivores. More important phylogenetically were *Dimetrodon*, *Haptodus*, and their relatives, the dominant carnivores of the early Permian, from which the later therapsids appear to have been derived.

Therapsids.—These more advanced, mammal-like reptiles replace their ancestors, the pelycosaurs, as the common reptiles of the middle and late

Permian; they are abundantly represented in the Beaufort beds of South Africa and are present in Russia as well. The great dinocephalians, including the carnivorous titanosuchids and the herbivorous tapinocephalids, are confined to, and common in, the Middle Permian; some of the Russian types appear to be slightly older in time of appearance and somewhat more primitive than those of South Africa. Dicynodonts are present in the Middle Permian of South Africa but were relatively small and rare; in the Upper Permian these nearly toothless herbivores are the commonest of vertebrates. There is, in addition, a variety of more progressive carnivores, gorgonopsians, and therocephalians, in the Middle and Upper Permian of South Africa and the Upper Permian of Russia.

Other reptiles.—It is curious that in the Permian there are few evidences of the ancestry of the reptilian groups which were to become prominent in the Mesozoic. *Eunotosaurus* of the Middle Permian of South Africa is a possible forerunner of the turtles; there are no clues as to the ancestry of the ichthyosaurs. Of the synaptosaurs, we find no forms resembling the aquatic sauropterygians of the Mesozoic, but there are a number of relatively rare protorosaurs, such as *Araeoscelis* of the American red beds and *Protorosaurus* of the European Kupferschiefer. Diapsid reptiles are notably absent in the Lower and Middle Permian; in the Upper Permian of South Africa, however, there appear a number of small primitive eosuchians, such as *Youngina*.

The late Pennsylvanian or early Permian witnesses the only appearance of that problematical order of small aquatic reptiles, the Mesosauria. *Mesosaurus* is known from the Dwyka of South Africa and an equivalent formation across the South Atlantic in Brazil; no trace of this group has ever been found in northern continental deposits.

Gondwanaland.—In all three southern continents and in peninsular India as well, sediments of similar types are found in the late Paleozoic and early Mesozoic; in all three continents there is evidence of pronounced glaciation in late Carboniferous or early Permian time; in all these areas there is found a common flora characterized by the genera *Glossopteris* and *Gangamopteris*. This has led to a belief that these regions were then parts of a common land mass named Gondwanaland, separated from the Eurasian land areas by an east-west Tethys Sea. The distribution of the vertebrate life of the Permian, especially the Karroo therapsid fauna, has been held to support this theory. We have noted, however, that in the Middle and Upper Permian, in which therapsids are numerous in South Africa, there are few known vertebrates of any sort in the deposits of North America and in most of Europe. And we have further noted that the one good northern fauna of the later Permian, that of Russia, is highly comparable to that of South Africa. The therapsids thus furnish no proof of the union and joint isolation of the southern continents. The only favorable evidence for this theory furnished by the vertebrates is the presence of *Mesosaurus* on both shores of the South Atlantic.

Permian: summary.—The chief characteristics and events of Permian vertebrate history are: (1) the disappearance during the period of many types of fishes, including cladoselachians, acanthodians, bradyodonts, and primitive crossopterygians; (2) continued dominance of palaeoniscoids and first appearance of the Holostei; (3) disappearance of most of the amphibian types and survival (as far as known) only of rhachitomous labyrinthodonts; (4) abundance of cotylosaurs; (5) dominance throughout of synapsid reptiles—pelycosaurs in early times, therapsids in the later Permian; and (6) presence of rare representatives of other reptilian groups.

The Paleozoic as a whole.—In the Paleozoic is included by far the greater portion of the vast period of time which has elapsed since life first appeared in abundance. From the point of view of the student of invertebrates, the Paleozoic may form a not unnatural unit, since most of these various lower-animal groups appeared full fledged at its beginning and at its close underwent marked change. But with the vertebrates it is otherwise; these forms appeared at a relatively late date and evolved rapidly through a series of progressive stages; and at the end of the era our story is broken, so to speak, in the middle of a sentence. Looked at in its broadest outlines, the history of vertebrates in the Paleozoic is not that of a single chapter in their development but of two full cycles and the beginning of a third.

A first major phase in vertebrate history seemingly occurred in the earlier half of the Paleozoic. The earliest vertebrates are imperfectly known except at the very end of the cycle—at the Silurian-Devonian boundary. The vertebrates were then a rather obscure group of small, bottom-living river dwellers, playing but a minor part in the drama of life-development. Their lack of biting mouth parts rendered impossible the trituration of food of any degree of size or toughness; this appears to have been a major factor militating against their development. Mud-grubbers they were, and mud-grubbers, seemingly, they were destined to remain.

But apparently toward the end of the Silurian there took place a great advance in vertebrate structure which initiated a new cycle in the history of the group. This advance was the development of jaws; from this resulted a true conquest of the waters by vertebrates. With the development of jaws and teeth came the possibility of a predaceous existence, and active swimming succeeded the sedentary bottom-dwelling habits of the ancestral types. Jawed fishes were exceedingly abundant in fresh waters before the Devonian was far advanced and were widespread in the oceans in the Carboniferous, although a decisive and permanent conquest of the salt waters was not made until Mesozoic times. To this great cycle of aquatic conquest belongs the development of the amphibians as well, for lungs and tetrapod limbs seem originally to have been merely adaptations for a more successful life in inland waters.

In the Carboniferous there took place a second great advance among the more progressive vertebrates, resulting in the initiation of a third stage in their history. This advance was the release of tetrapods from the water through changes which eliminated the aquatic stage in individual development. The resulting new cycle of development was the conquest of the land by the reptiles.

Primitive reptiles, little known in the Carboniferous, were abundant by the beginning of the Permian. Most of them were members of two ancient groups—the cotylosaurs, stem stock of all true land vertebrates, and the synapsids, destined to give rise to mammals. The close of the Paleozoic still saw these two groups dominant. Only in the Triassic did this archaic land radiation come to an end and these forms give way to newer reptilian types which held sway during the rest of the Mesozoic.

CHAPTER 28

MESOZOIC VERTEBRATES

THE Mesozoic era is usually known as the Age of Reptiles, for it was during this time that there flourished the great reptilian groups now extinct: the varied dinosaurs on land, the flying reptiles in the air, and ichthyosaurs, plesiosaurs, and other marine types in the seas. The Mesozoic witnessed, as well, the more modest beginning of existing reptile groups—turtles, lizards, snakes, crocodiles. Further, it was during this era that birds and mammals, both derived from reptilian ancestors, made their appearance. Among amphibians the Mesozoic sees the change from old to new—extinction of the labyrinthodonts and appearance of typical frogs and urodeles. And although our attention naturally centers on higher groups, the fishes of the Mesozoic had an interesting development. During this time there developed modern groups of sharks and rays and the chimaeras; the ray-finned bony fishes progressed from the chondrostean to the holostean grade of evolution and finally to the modern teleost type.

TRIASSIC

The Triassic forms an introduction to the Mesozic vertebrate story. At its beginning we find faunas both on land and in the water comparable to those of the late Paleozoic. During the period, however, there were marked changes among both fishes and reptiles; by the close of the Triassic there had appeared almost every one of the striking vertebrate groups which were to play major roles in the Mesozoic story.

Vertebrate beds.—The Triassic owes its name to the sequence of fossiliferous deposits characteristic of the period in central and western Europe. It opens with the Bunter—variegated continental beds with sparse vertebrate remains, deposited on the northern shores of the seas covering the present Alpine region. These seas advanced northward; their sediments form the Middle Triassic Muschelkalk, a limestone group with a rich fauna. In the Upper Triassic, with retreating seas, there is a return to dominantly continental beds in the Keuper, a series mainly red in color, supposedly deposited under arid conditions and with a good assemblage of vertebrate remains. The Upper Triassic closes with the Rhaetic, forming a transition to the Jurassic and including a number of bone beds. The Triassic areas described are best developed in southern Germany and adjacent regions; Middle and early Upper Triassic aquatic vertebrates are abundant at Perledo and other localities in the southern foothills of the Alps, and the Upper Triassic is represented in the Bristol district of Great Britain.

A second important Triassic sequence is that of South Africa. The earlier Triassic, poor in fossils in most of Europe, is here represented by the richly fossiliferous upper zones—*Lystrosaurus*, *Procolophon*, *Cynognathus*—of the Beaufort series. The succeeding Stormberg Series covers the remainder of the Triassic; the Middle Triassic beds (Molteno) are barren (except for plants), but the Red Beds and Cave Sandstones of the Upper Triassic have yielded vertebrates similar to those of the Keuper and the Rhaetic.

Productive Triassic areas of lesser vertical range and lesser importance are scattered through every continent. In eastern Australia deposits with rich fish faunas—Narrabeen, Hawkesbury, Wianamatta—are found at several Triassic horizons. Triassic beds important for fishes and amphibians are found in Greenland, Spitzbergen, eastern Russia, Madagascar, and India. More continental types of deposits comparable to those of the South African Lower Triassic are found in several localities in eastern Asia, and phases (Middle Triassic?) of the same fauna are seen in East Africa and the Rio do Rasto beds of southern Brazil.

Marine faunas of Middle and Upper Triassic age, more or less comparable to those of the Muschelkalk, are to be found in Spitzbergen and in Nevada and California. Upper Triassic continental deposits similar in faunal content, and even in their red color, to the Keuper and Stormberg, are plentiful in North America. They include the Newark series of the Atlantic Coast (famous for footprints), the Chinle, Dockum, and Chugwater of the West. Similar red beds are present in eastern and southern Asia as well.

Fishes.—We have noted a marked decrease in the numbers and variety of fishes present in the last phases of the Paleozoic: placoderms had become extinct, the Chondrichthyes and Choanichthyes were reduced to a few types, and only the actinopterygians had remained in a flourishing condition. This situation still prevailed in the Triassic. Of the cartilaginous fishes, primitive chimaeras descended from the bradyodonts were presumably present but are known only from a single poor and questionable specimen; the last lingering pleuracanths are found in the fresh-water Triassic of Australia; *Hybodus* and a few related shark types are the only known chondrichthyan inhabitants of the Triassic seas. Of the Choanichthyes, the typical crossopterygians were extinct, but the coelacanths had survived and were apparently beginning to change their habitat from fresh waters to salt; *Ceratodus* represents the lungfishes and is abundant in some formations presumably deposited under arid conditions.

The history of actinopterygian dominance and progress seen in the later

TABLE 3

Mesozoic Vertebrate Localities

	European Stages	Europe	North America	South America	Asia	Africa	Australia
Cretaceous	**Upper Cretaceous inc. Danian, Maestrichtian, Senonian, Turonian, Cenomanian**	Transylvania dinosaur beds; Chalk of S. Eng., Belg., Maestricht (Neth.), N. France, Westphalia *M*[*]	Lance, Edmonton, Belly R. (Alberta-Mont.-Wyo.); Fruitland, Kirtland, Ojo Alamo (N.M.); Niobrara (Kan.) *M*; Pierre (S.D.) *M*; Chico (Calif.) *M*; Austin chalk (Tex.) *M*; Monmouth, Matawan (N.J.) *M*; Selma (Miss.) *M*	Red Beds of Patagonia; Uruguay; Ceara (Brazil) *M*	Djadochta (Mongolia); Lameta series, Trichinopoly and Ariyalur stages (Ind.); Mt. Lebanon (Syria) *M*	Baharije stage (Egypt); Madagascar	Opal beds (N.S.W.); New Zealand *M*
	Lower Cretaceous, inc. Albian, Aptian, Neocomian	Wealden (Eng., Belg., Hanover); Neocomian of Voirons (Switz.), Istria, etc., *M*; L. Greensand, Gault of Channel region (Eng.) *M*	Cloverly (Wyo.); Arundel (Md.)	Neuquem fm. (Arg.); Bahia (Brazil) *M*	Iren Dabasu, Oshih, Ondar Sair, (Mongolia); Shantung (China)	Uitenhage (S.Af.)	Tambo ser., Rolling Downs (Queens.)
Jurassic	**Upper Jurassic=Malm or U. Oölites inc. Purbeckian, Portlandian, Kimmeridgian, Oxfordian, Callovian**	Purbeck beds (Eng.); Lithographic ls. of Solenhofen, Kelheim (Ger.), Cirin (France) *M*; Oxford clays and Kimmeridge beds of S. Eng. and N. France *M*	Morrison fm. of western states (Como, Lost Cabin, Vernal, etc.); Sundance (Wyo.) *M*; western Cuba *M*			Tendaguru (E.Af.)	
	Middle Jurassic=Dogger or L. Oölites, inc. Bathonian, Bajocian	Stonesfield slate, Forest Marble (Eng.)	Navajo ss. (Ariz.)			Madagascar	
	Lower Jurassic=Lias, with var. subdivisions	Lias of Yorkshire, Dorset (Eng.), Caen region (France), Holzmaden, etc. (Bavaria) *M*	Wingate (Ariz.)				Talbraggar (N.S.W.); Lower Walloon, Durham Downs (Queens.)
Triassic	**Rhaetian, Norian**	Rhaetic bone beds (S.W. Eng., S. Ger., Scania); Keuper and Lettenkohle (Ger.); Alpine region (Perledo, etc.) *M*	Chinle (Ariz.); Chugwater (Wyo.); Dockum (Tex.); Newark ser. (Mass.–N.C.); Hosselkus ls. (Calif.–Nev.) *M*		Maleri (Ind.); red beds of Yünnan	Cave Ss. and red beds of Stormberg series (S.Af.)	Wianamatta inc. St. Peter's beds (N.S.W.)
	Carnian, Ladinian	Muschelkalk of Germany and equivalents in Alpine region (Besano, etc.) *M*; Spitzbergen *M*	Shinarump (Ariz.); W. Humboldt Range (Nev.) *M*	Rio do Rasto group (Brazil)	Shansi (China)	Upper Ruhuhu bone bed, Manda beds (E.Af.)	Hawkesbury beds of Brookvale, etc. (N.S.W.)
	Anisian, Scythian	Bunter of Central Europe; "Zone V" of N.E. Russia (Vetlugian); Mt. Bogdo (Russia); Spitzbergen *M* (in part)	Moenkopi (Ariz.); E. Greenland *M* (in part)		Sinkiang; Luang Probang (Indo-China); Mangli, Panchet (Ind.)	*Lystrosaurus*, *Procolophon*, and *Cynognathus* zones of U. Beaufort (S.Af.); Madagascar *M*	Narrabeen, inc. Gosford (N.S.W.)

[*] *M* = marine.

Paleozoic is continued in the Triassic. The primitive palaeoniscoids are still prominent. The characteristic ray-fins of the times, however, are those to which the term "subholosteans" is applied—forms progressive in character, structurally intermediate between palaeoniscoids and holosteans, and probably giving rise, in polyphyletic fashion, to many families of the latter group. There are perhaps half-a-hundred genera and half-a-dozen families of subholosteans in the Triassic—*Dictyopyge*, *Redfieldia* [*Catopterus*], *Perleidus*, *Saurichthys*, and *Cleithrolepis* are representative. By the end of the period, however, the subholosteans were becoming much reduced in numbers and were giving way to typical holosteans—such as *Semionotus* and *Eugnathus*—which were to dominate in the Jurassic.

With few exceptions the older actinopterygians were fresh-water forms. We have noted, however, that in the later Permian many palaeoniscoids appear to have existed in brackish waters. In the Triassic a strong trend is apparent among ray-fins toward a marine existence. From this time onward the sea is the major center of actinopterygian life and evolution.

Amphibians.—The Rhachitomi had been the dominant Permian amphibian types; almost all the amphibians in the earliest Triassic beds are members of the same group but are "neorhachitomous" forms approaching the Stereospondyli in structure. The stereospondyls, although destined to become extinct at the close of the Triassic, flourished greatly for the time. They included *Trematosaurus* and other long-snouted fish-eaters of the early Triassic; the capitosaurs, prominent throughout the period; the metoposaurs such as *Buettneria*, with anteriorly placed orbits, abundant in the American Upper Triassic; the short-skulled brachyopids. An important document is the lone specimen of the primitive "frog," *Protobatrachus*, from the Triassic of Madagascar; urodele ancestors are known neither in this period nor in the Jurassic.

Primitive reptile groups.—In reptilian evolution, the Paleozoic-Mesozoic boundary is almost without meaning. By the end of the Triassic there had appeared the typical reptilian groups that were to dominate the later Mesozoic; at the beginning of the period, however, the fauna was still essentially a Paleozoic one.

This archaic fauna is best represented in the South African Lower Triassic deposits and in a later phase in those of Brazil; finds from other areas are few, but enough to suggest that the South African fauna was one typical of most, if not all, of the lands of the early Trias.

Dominant in the early Triassic were the therapsids. Dicynodonts were still flourishing but restricted in variety; notable were large types such as *Kannemeyeria*, and a small amphibious genus, *Lystrosaurus*, widely distributed in the early Trias. Gorgonopsians and therocephalians were extinct and were replaced as carnivores by more progressive relatives or descendants—the cynodonts, such as *Cynognathus* and *Diademodon,* and the very advanced *Bauria* group. A few large dicynodonts survived into the late Triassic and seem to have been world wide in distribution. Otherwise, typical therapsids had disappeared by late Triassic times. Presumably descended from them were a number of obscure or aberrant late Triassic forms, the ictidosaurs, as *Tritylodon* and *Dromatherium,* advanced in nature and close to the mammalian evolutionary level.

Cotylosaurs are present in the form of *Procolophon* and its relatives, the last survivors of the order. The protorosaurs, too, are a group which had arisen in the Permian and persisted into various horizons of the Triassic, where they appear in the form of such odd types as *Trilophosaurus* and the peculiar, long-necked *Tanystropheus.*

Newer reptile groups.—Other reptile types, however, were making their appearance even in the Lower Triassic to mark the beginning of the new Mesozoic radiation of reptiles. The little eosuchians, which had been present in the late Permian, continue into the Triassic and are presumably ancestral to the rhynchocephalians. This last order is represented in the early Trias by a few rare primitive types; rhynchocephalians became more abundant later in the period and developed, in *Rhynchosaurus* and its allies, a peculiar, short-lived branch of rather large, strong-beaked reptiles. Turtles such as *Triassochelys,* characteristic, if somewhat primitive, members of their order, appear—seemingly suddenly—in the late Triassic.

Marine reptiles.—In the marine Trias (Muschelkalk) of Germany and in other formations of middle and late Triassic age in Spitzbergen and western North America, we see an early stage in the development of marine reptiles. A number of groups are already represented, and in no case have we any adequate knowledge of their ancestry. Most striking are the early ichthyosaurs, such as *Mixosaurus* and *Shastasaurus,* already well adapted for a marine life but somewhat less advanced than their Jurassic descendants in development of paddles and tail fin. Varied sauropterygians are present. Particularly common were the nothosaurs, forms already aquatic but much less specialized than the plesiosaurs which were to replace them in the Jurassic. The Triassic was the period during which there developed the placodonts—amphibious mollusk-eating sauropterygians with curious resemblances to the turtles. *Thalattosaurus* of the American Triassic is a poorly known marine reptile of obscure relationships.

Archosaurs.—The archosaurs, or ruling reptiles, were destined to be the dominant land vertebrates of the later Mesozoic; the stem order of this subclass, the Thecodontia, made its appearance with a few genera in the early Triassic and became prominent in the later part of the period but was destined to disappear at its close. Most representative of thecodonts were the pseudosuchians—small reptiles with bipedal tendencies, such as *Euparkeria* and *Ornithosuchus*. The phytosaurs are among the commonest of late Triassic fossils in northern continents—aberrant, long-snouted thecodonts adapted to a predaceous amphibious life. *Protosuchus* of North America and similar types from South Africa are transitional in structure between primitive thecodonts and the crocodiles which were to replace the phytosaurs in the Jurassic.

Primitive dinosaurs.—By the latter part of the period the dinosaurs, evolved from the pseudosuchians, had made their appearance. Of ornithischians there is but a single rather dubious fragment from South Africa, but saurischians are abundant in Upper Triassic formations, particularly in Europe and South Africa. A number were small, lightly built coelurosaurians, such as *Podokesaurus* and *Saltopus*. *Teratosaurus* is typical of a series of large forms leading to the large carnivores of the Jurassic. A third type, of which *Yaleosaurus* ("*Anchisaurus*") and *Plateosaurus* are representative, consists of heavily built dinosaurs which are the ancestors of the huge Jurassic sauropods.

Triassic: summary.—The vertebrate life of the Triassic is characterized by (1) rarity of cartilaginous fishes; (2) replacement of chondrosteans by holosteans as the dominant fish group; (3) a trend toward marine life on the part of bony fishes; (4) last appearance of the labyrinthodonts; (5) appearance of rhynchocephalians and turtles; (6) development of primitive reptilian marine life, including ichthyosaurs and varied sauropterygians; (7) the abundance and radiation of the thecodonts, followed by their extinction; (8) appearance and rapid development of the theropod dinosaurs; (9) extinction of typical mammal-like reptiles, but (10) persistence of forms perhaps transitional to mammals (ictidosaurs).

JURASSIC

The Jurassic was a time of widespread seas and reduced land areas. For most of the duration of the period the principal deposits are of marine origin, and it is only toward the close of the Jurassic that continental sediments become prominent. In consequence, our knowledge of aquatic vertebrates is much more complete than is that of terrestrial forms.

Vertebrate localities.—The typical European Jurassic section is almost exclusively marine in nature. The Lower Jurassic—the Lias—contains numerous localities rich in marine vertebrate remains, particularly on the Yorkshire coast; the region of Lyme Regis on the English Channel; the opposite coastal region of Normandy; and in southern Germany, particularly the famous Holzmaden quarries in Bavaria. The later European Jurassic—frequently termed the Dogger and Malm or (combined) the Oölites—in general contains far fewer remains of vertebrates. There are, however, important exceptions. The Oxford and Kimmeridge clays are rich in fish and reptilian remains. Prominent late Jurassic localities are the lithographic limestone deposits of Solenhofen and Kelheim in Germany and Cirin in France. Here fine-grained sediments, presumably laid down in quiet, coral-reef lagoons, have preserved numerous specimens of fishes and occasional tetrapod intruders. Jurassic marine deposits are present in other parts of the world and may occasionally produce vertebrates.

Land vertebrates are, in general, notable for their absence. A few are present in the marine European records, as at Solenhofen, and in Middle and Upper Jurassic estuarine localities in England, at Stonesfield, and in the Purbeck beds. An abundant record of terrestrial forms is found only at the very end of the period and then only in two regions. The Morrison beds, exposed over large areas of western North America from Montana through Wyoming to Utah, Colorado, and even Oklahoma, appear to have been laid down under conditions similar to those of the modern Mississippi delta and contain a particularly rich dinosaur fauna. Very similar in nature and in fauna are the Tendaguru beds in Tanganyika Territory, East Africa.

Fishes.—The Jurassic, with seas full of invertebrate food, saw the beginning of a great recrudescence of cartilaginous fish life. There appear, in the Lias, *Squaloraja*, *Myriacanthus*, and other primitive members of the mollusk-eating chimaeras, destined to play a modest part in marine life from this time forth. Much more important were developments among the selachians. From the surviving hybodonts there began to branch off various types of modern sharks. *Heterodontus* and *Hexanchus*, relatively primitive living forms, had appeared before the end of the Jurassic, as had half-a-dozen genera representing more modern shark families. Somewhat slower to develop were the skates and rays, but the guitarfish, *Rhinobatis*, a primitive skate type, was already evolved by the late Jurassic.

Of fresh-water bony fishes we know almost nothing. The sea, however, was swarming with members of this class. Apart from *Undina* and a few other coelacanths, all these forms were actinopterygians. There were surviving palaeoniscoids; the earliest sturgeon, *Chondrosteus;* and a few subholosteans. Almost all, however, were holosteans. The semionotids *Dapedius* and *Lepidotus;* pycnodonts such as *Gyrodus* and *Microdon; Aspidorhynchus;* amioids such as *Caturus*, *Eugnathus*, *Pachycormus*, and *Macrosemius;* advanced types such as *Pholidophorus*—these are but a few of the many common forms. And, in addition, we find, particularly toward the end of the period, swarms of small primitive teleosts, such as *Leptolepis*, which herald the approaching rise of this final major division of the ray-finned fishes.

Amphibians.—The Jurassic marks the low point in our knowledge of amphibian life. Unless a doubtful fragment from Australia belongs to a labyrinthodont, we have only a few bits of frog remains to represent the entire class.

Marine reptiles.—The nothosaurs and placodonts and the obscure thalattosaurs of the Triassic were absent in Jurassic waters, but the seas contained an abundance of marine reptiles. The ichthyosaurs of the period were far advanced in their readoption of a fusiform fish body and very fishlike fins. In the Lias they appear already to have reached the peak of their development. Most of the ichthyosaurs of the period have been included in the single genus *Ichthyosaurus,* but they appear to have actually included a wide range of genera varying in paddle and jaw development; *Eurhinosaurus,* for example, is a form closely analogous to the modern swordfish. The sauropterygians are represented by a variety of plesiosaurs, including short-necked types, such as *Pliosaurus* and *Peloneustes*, and more abundant longer-necked genera, such as *Plesiosaurus* and *Cryptocleidus.* The only instance of invasion of the seas by the archosaurs is the development in the later Jurassic of the short-lived group of marine crocodiles, such as *Metriorhynchus* and *Geosaurus.*

Dinosaurs.—But few remains of land vertebrates are known from the earlier marine deposits of the period; most of our knowledge of dinosaurs is gained from the faunas of the Morrison of North America and the Tendaguru beds, both of late Jurassic age. By this time the dinosaurian groups had developed in spectacular fashion. Among the saurischians, the coelurosaurs were present in forms of modest size, as *Compsognathus* and *Ornitholestes.* Other bipeds had, however, increased in size to produce such large types as *Allosaurus, Ceratosaurus,* and *Megalosaurus.* Parallel to this development had been the evolution of their gigantic cousins, the amphibious sauropods. These appear to have been at the peak of their development in the late Jurassic—*Diplodocus, Apatosaurus* [*Brontosaurus*], *Camarasaurus, Cetiosaurus,* and *Brachiosaurus* are among the familiar names.

The development of the ornithischians appears to have been a slower process than that of the saurischians. But by the time of deposition of the Morrison and its equivalents a variety of these forms was in existence. Most were bipedal ornithopods of relatively small size, of which *Camptosaurus* is representative. A striking Morrison form is the quadruped *Stegosaurus,* with a double row of plates and spines on its back; *Kentrurosaurus* is a closely related East African genus.

Other reptiles.—Our knowledge of the smaller reptiles of the Jurassic is very limited. We find a variety of turtles, mainly of the primitive amphichelydian group but including, in *Thalassemys* and its allies, primitive forerunners of the cryptodires. Most were presumably amphibious in nature; it is possible that some were well along in adaptation to marine existence.

Homoeosaurus is a small Jurassic reptile exceedingly close to the surviving rhynchocephalian *Sphenodon* of New Zealand; *Pleurosaurus* and *Sapheosaurus* are small types of doubtful position but often included in the Rhynchocephalia. Lizards, related to this last order and, like them, presumably derived from an eosuchian stock, first appear in the form of two rare Upper Jurassic genera.

Crocodiles are abundant as fossils. We have already noted the development of a marine group; there were four other families showing more normal amphibious structures. All were in the mesosuchian stage of evolution, with the palate less developed than in modern forms.

The Jurassic was the time of the appearance and greatest development of the pterosaurs. In the Lias several genera of long-tailed forms, such as *Dimorphodon*, are present and are already completely adapted for flight. In the late Jurassic long-tailed pterosaurs, such as *Rhamphorhynchus*, are still abundant, but we find, in addition, numerous specimens of *Pterodactylus*, with a short tail and more elongated wings.

Birds.—Our first glimpse of bird life comes from two specimens, *Archaeopteryx* and *Archaeornis*, from the Solenhofen Upper Jurassic lithographic stone. It is certain that birds are of thecodont derivation, but earlier stages in their development are unknown and would be difficult to recognize if found in the absence of feathers. These typical avian structures are here present to prove the nature of the specimens despite their retention of teeth, long bony tails, and typically dinosaurian "arms."

Mammals.—We have noted in the late Triassic the presence of rare and obscure forms which are seemingly transitional to mammals, and some of which may perhaps belong to this group. In the Jurassic, mammals of primitive but varied types are definitely present; they are, however, small, rare, and fragmentary. Almost all known specimens come from three sites—Stonesfield in the Middle Jurassic of England, the late Jurassic Purbeck beds of that country, and a single small pocket in the Morrison at Como Bluff, Wyoming. In the Stonesfield locality there is a seeming survivor of the tritylodont group; its definitely mammalian fauna is extremely limited and includes but two triconodonts and a single pantothere, *Amphitherium*. The two Upper Jurassic sites have a much more extensive fauna; those of the two sides of the Atlantic show relatively small differences from one another. There are further triconodonts and numerous pantotheres; the symmetrodonts make their only known appearance at this time. *Plagiaulax* and several relatives are the earliest representatives of the curious aberrant multituberculates, destined to persist to Eocene times.

Jurassic: summary.—Prominent features of Jurassic vertebrates were: (1) among fishes, the height of the holostean supremacy, the appearance of the first teleosts and the beginning of the radiation of modern elasmobranch types; (2) appearance of frogs, first of the modern amphibians; (3) among dinosaurs, the continued expansion of bipedal types in both orders and the evolution of armored forms and of sauropods; (4) a great development of marine reptiles, especially ichthyosaurs and plesiosaurs; (5) appearance of lizards, typical crocodiles, and pterosaurs; (6) the first birds; (7) development of small primitive mammals of several types.

CRETACEOUS

The Cretaceous is among the longer periods of the earth's history; by some authors it is divided into two periods, the Comanchean and the true (Upper) Cretaceous. This scheme will not be followed here, but there is considerable contrast between the vertebrates of the earlier and the later parts of the period.

Vertebrate localities.—Lower Cretaceous marine life is best represented in the Neocomian beds of Europe (particularly Dalmatia), and there are equivalent deposits containing fish faunas and occasional aquatic reptiles in North America, Bahia (Brazil), and other regions. Much more prolific are Upper Cretaceous marine beds: the Chalk and related deposits of southern England and Westphalia; the similar Niobrara Chalk of North America; Australian marine deposits; Ceará (Brazil); etc. Notable are the limestones of Mount Lebanon, Syria, with a wealth of varied fishes.

In the Lower Cretaceous, continental deposits are none too abundant. The Wealden of southern England, northern France, and Belgium has a terrestrial fauna of very early Cretaceous age, and there are other, if less important, areas of this age in North America and in China and Mongolia. In the Upper Cretaceous the most famous of continental formations are the great dinosaur beds of western North America—Belly River, Edmonton, Lance, and equivalents—which extend over great areas from Alberta down the flanks of the Rockies to New Mexico. In Europe, Upper Cretaceous continental sediments are rare, except for an area in Transylvania. Dinosaur faunas are, however, present in India, China, and Mongolia and in a variety of localities in the southern continents—Patagonia, South Africa, eastern Australia.

Fishes.—The selachians have expanded greatly. The stem hybodonts make their final appearances in the Cretaceous. Their descendants are numerous. Of some sixteen or so families of living sharks, all but four had representives in the Cretaceous seas. Many of the genera living today, such as *Carcharias, Isurus, Carcharodon, Galeocerdo,* etc., were already identifiable; since the opening of the Jurassic the major part of modern shark evolution had been accomplished. The skates and rays had also reached essentially modern conditions before the end of the Cretaceous, and there were already present such familiar living types as *Pristis,* the sawfish; *Raja,* the common skate; *Trygon,* the sting ray; and *Myliobatis,* the great eagle ray.

In the Cretaceous, *Mawsonia* and a few other rare types are the last of fossil coelacanths and were, indeed, thought to represent the termination of crossopterygian existence before the recent discovery of a living coelacanth. This period sees the replacement of the holosteans by the teleosts as the dominant group of fishes. Of lower actinopterygians, the seas contained the last rare palaeoniscoid and a few holosteans. Most of these last disappeared before Upper Cretaceous times, and only the pycnodonts remained in a flourishing condition. The teleosts were diversifying rapidly and replacing them. Most typical of Cretaceous teleosts were primitive isospondyls, clupeoids related to the tarpons and herrings. Early Cretaceous genera were few, but in the late Cretaceous there were swarms of such fishes, some (as *Portheus*) of very considerable size. More advanced groups were quick to make their appearance. In the Upper Cretaceous more specialized isospondyls of various types were present. A dearth of fresh-water deposits is perhaps responsible for our lack of knowledge of the important Ostariophysi—the carp-catfish group. There are, in the Upper Cretaceous, primitive eels, representatives of the deep-sea groups of Heteromi and Iniomi, and even of the great group of the Acanthopterygii. These spiny-finned fishes are, however, rare and include but a few genera of berycoids, perches, mackerels, pompanos, and a member of the specialized plectognaths.

Amphibians.—To the meager record of the history of modern amphibian groups, we may add in the Cretaceous the first appearance of urodeles.

Marine reptiles.—Aquatic reptiles continue in abundance in the Cretaceous, although with some change in the membership of the groups concerned. The marine crocodiles disappeared early in the period. Ichthyosaurs, although seemingly highly adapted to a marine life, were on the downgrade. They appear to have become quite rare by Upper Cretaceous times; not a one, for example, has ever been found in the richly fossiliferous Niobrara Chalk of North America. Plesiosaurs, on the other hand, flourished vigorously, and the Upper Cretaceous chalk deposits contain abundant remains of a score of genera, among which *Polycotylus*, *Trinacromerum*, and *Elasmosaurus* are familiar forms; *Kronosaurus* of Australia, with a skull nearly 10 feet long, was the giant of the order.

The turtles, amphibious by nature, took to the sea in Upper Cretaceous times. Several families of cryptodires, including such genera as *Archelon*, *Protostega*, and *Toxochelys*, adopted this habitat and tended to modify themselves to it by paddle-like limb developments and lightening of armor.

Another interesting Cretaceous development was the appearance of marine lizards. In the Lower Cretaceous of Europe, *Dolichosaurus* and *Aigialosaurus* are representatives of monitor-like lizard families which were becoming adapted to an aquatic habitat. From such forms sprang the mosasaurs, such as *Mosasaurus* of Europe and *Tylosaurus* and *Clidastes* of North America, large and common predaceous reptiles of the Upper Cretaceous.

Dinosaurs.—Of Lower Cretaceous dinosaurs we know but little, apart from those of the Wealden of western Europe, where *Iguanodon*, a large ornithopod, was common, and of eastern Asia, where carnivores, sauropods, and ornithopods were present. Apparently, the fauna was, in general, similar in content to that of the Morrison.

Late Cretaceous dinosaur beds are highly developed in western North America, and more scattered beds and finds are present in every other continent. In many respects this Upper Cretaceous fauna is a very different assemblage from that seen a period earlier. Coelurosaurs still survive, but even these slenderly built saurischians have tended to grow in size and specialize into such forms as the toothless ostrich dinosaur, *Struthiomimus*. The larger carnivores are now represented by ponderous giants, such as *Tyrannosaurus* and *Gorgosaurus*. The sauropods had regressed in numbers and variety during the Cretaceous. Among all the numerous dinosaur finds from North America, there are but two fragmentary specimens of these amphibious forms. It appears, however, that this paucity of sauropods is less pronounced in other regions, for there are a number of records of *Titanosaurus* and related sauropods from the Upper Cretaceous of the Southern Hemisphere and even in India and China.

Ornithischians abound in the Upper Cretaceous. Little *Thescelosaurus* is a survivor of a very primitive ornithopod group. Of these bipeds, however, the dominant forms of the times were the amphibious duckbills, the hadrosaurs or trachodonts, abundantly represented by a score of genera which show numerous variations in the curious crests which frequently crown their heads. The stegosaurs had disappeared but have been replaced by another group of armored dinosaurs—*Ankylosaurus* and related types, low-bodied, large-skulled genera covered with a solid dorsal armor of bony plates. A final group of ornithischians is that of the horned dinosaurs, the ceratopsians, with a bony neck frill in the primitive genus *Protoceratops* and with large horns developed in addition in more progressive genera, such as *Triceratops* and *Monoclonius*.

Other reptiles.—Turtles are numerous in Upper Cretaceous deposits. Many are still amphichelydians of Mesozoic type, but representatives of the two existing suborders are present as well. There are a few pleurodires, including even representatives of the living South American genus *Podocnemis*. More numerous are cryptodires. In addition to the marine forms already mentioned and survivors of the Jurassic *Thalassemys* group, there are relatives of the living marsh turtles and the soft-shelled trionychids. There is almost no evidence of rhynchocephalians. Sometimes placed in this order but of doubtful position is *Champsosaurus*, a small, long-snouted amphibious diapsid of the late Cretaceous and earliest Tertiary. In the Upper Cretaceous, lizards are, for the first time, abundant as fossils. Apart from the mosasaurs, half-a-dozen families are represented, including forms typical of most of the major subdivisions of the group. In this period, too, there arises the last of the reptile groups to make its appearance—the snakes, represented by the rare and primitive types *Pachyophis* and *Simoliophis*.

As in the Jurassic, the crocodiles are well represented. Most are still in the mesosuchian stage of development, but there are a number of more progressive genera leading to the modern crocodiles and alligators.

Pterosaur remains are rare except in the Niobrara Chalk of the Upper Cretaceous. The rhamphorhynchoid type is extinct, and by the Upper Cretaceous we find surviving only short-tailed pterodactyloids, such as *Nyctosaurus* and the giant, toothless *Pteranodon*.

Reptilian extinction.—By the end of the Cretaceous the greater part of the reptilian life of the Mesozoic had become extinct—all ichthyosaurs, all sauropterygians, all the dinosaurs and pterosaurs. Surviving into the typical Cenozoic we find only the turtles, lizards, snakes, crocodilians, and a lone rhynchocephalian. We must not overemphasize the rapidity of this extinction; for some of the groups—such as the ichthyosaurs and perhaps the pterosaurs—had become reduced in numbers well before the end of the period. Many dinosaur groups, however, appear to have flourished greatly in very late Cretaceous deposits, and their extinction at the Mesozoic-Tertiary boundary is one of the most dramatic events in vertebrate history.

The reasons for this reptilian catastrophe have been much debated, and the causes may have been complex in nature. It has, however, been reasonably argued that geological processes may be, in great measure, fundamentally responsible. In the late Cretaceous there came about the Laramide revolution, a time of mountain-building during which there began the elevation of the Rockies and other mountain chains. This condition of rising lands might well have affected markedly the more amphibious dinosaur groups, such as the sauropods and duckbills, by limiting the areas of the swamps and lagoons in which they made their livelihood. Food materials, too, would be affected, for these geological disturbances brought about climatic shifts, which are seen reflected in marked changes in vegetation in the late Cretaceous. Many herbivores are narrowly restricted in their diets, and floral changes may be responsible for much extinction. Finally, the disappearance of carnivores would inevitably follow the disappearance of the herbivores upon which they fed.

The reasons for the elimination of marine forms are more difficult to deduce. It may be, however, that the replacement of holostean fishes by progressively higher and presumably more efficient teleost types was a factor, in addition to changes in invertebrate life.

Birds.—There is a gap in our history of birds between the late Jurassic and the late Cretaceous. Even in deposits of the latter age our knowledge of birds is almost entirely confined to oceanic or water-dwelling forms, such as the ternlike *Ichthyornis* and the swimmer *Hesperornis* of the Niobrara Chalk. These were typically birdlike in most skeletal features, but they still retained teeth. Possibly, however, other diversified and progressive forms may have been included in the unknown inland avifauna.

Mammals.—Of Lower Cretaceous mammals we know exactly three teeth (of a multituberculate). In the late Cretaceous, mammals are again found but are restricted almost entirely to a few localities in the Lance formation of Wyoming and to one in Mongolia. The fauna is markedly different from that seen in the Jurassic. The multituberculates are still present and are plentiful, but the other Jurassic orders—triconodonts, symmetrodonts, and pantotheres—have disappeared. The common types are marsupials, some strikingly similar to the living opossums. And, in addition, there are a few primitive placentals, prophetic of the emergence of this group in Tertiary days.

Cretaceous: summary.—Among the principal features of Cretaceous vertebrate history may be cited the following: (1) among fishes, further deployment of the selachians and a dwindling in importance of the holosteans, which were being replaced by primitive teleosts; (2) appearance of the first urodeles; (3) among marine reptiles, continued importance of plesiosaurs, appearance of marine lizards and turtles, reduction of ichthyosaurs; (4) progressive modernization of the crocodiles and turtles and development of primitive snakes; (5) climax in size of pterosaurs; (6) among dinosaurs, development of the largest carnivores, dwindling importance of sauropods, appearance of duck-billed ornithopods, heavily armored ankylosaurs, and horned dinosaurs; (7) birds reaching modern development except for the retention of teeth; (8) replacement of most Jurassic mammal groups by small primitive marsupials and placentals; (9) and, finally, the complete extinction by the end of the period of most of the characteristic reptilian types of the Mesozoic, including all the dinosaurs, the ichthyosaurs, plesiosaurs, marine lizards, and pterosaurs.

Mesozoic history.—The reptiles are the most interesting and most important vertebrates of the era. The Mesozoic includes the full cycle of existence of many major reptilian types—the dinosaurs, pterosaurs, and the varied marine reptiles—as well as the age of origin and expansion of still surviving groups, such as the turtles, lizards, and crocodiles. But it includes as well, in the early Triassic, the close of an earlier cycle in reptilian history which had begun near the end of the Carboniferous, with cotylosaurs and mammal-like reptiles as its chief characters. The earliest Mesozoic is an age of transition from the old to the new. On the other hand, the end of the era is a seemingly natural point of cleavage as regards vertebrate life.

With other groups, too, it seems that the Mesozoic includes not merely one typical cycle but, at its beginning, the final chapter in the old order. Among the bony fish the palaeoniscoids were still dominant at the beginning of the Triassic, just as they had been since the beginning of the Carboniferous. Before the close of the Mesozoic not only had the holosteans replaced them, but they in turn had been driven into insignificance by the progress of the teleosts. Again, the only known Triassic amphibians were the last survivors of the old labyrinthodonts of the Paleozoic, and only in the Jurassic and Cretaceous do we find the first characteristic members of the modern groups. Among cartilaginous fishes, also, the Triassic was a transitional period, while the Jurassic and Cretaceous witnessed a great revival in shark development. Primitive birds and primitive mammals were characteristic of the Mesozoic; but this, as far as our present knowledge goes, means merely the Jurassic and Cretaceous, for these groups are unknown in the Triassic.

The Triassic was thus a boundary period—a time of transition. In the Jurassic and Cretaceous we witness a full and characteristic Mesozoic life. And with the coming of the Cenozoic we enter a new age, the Age of Mammals.

CHAPTER 29

CENOZOIC VERTEBRATES

WITH the extinction of the great reptiles there began a new chapter in the history of land vertebrates. The mammals had until then remained small, rare, and inconspicuous but had seemingly progressed far in structural organization. Once the way was cleared, they emerged from obscurity and began a spectacular radiation into a host of types, many of which survive to the present day. The account of the Cenozoic given in this chapter will be based mainly on the history of the Mammalia; other groups are treated but briefly.

This last phase of the earth's history, comprising the Cenozoic era, is usually divided into a Tertiary period of considerable magnitude and a second period, the Quaternary, barely begun. The Tertiary may be divided into some five epochs—Paleocene, Eocene, Oligocene, Miocene, and Pliocene; the Quaternary includes only the short Pleistocene epoch and Recent times. These divisions are based in most cases upon the degree of modernity reached by invertebrates in European marine deposits. In Europe these epochs have been subdivided into a series of ages listed in Table 4. In many instances the terrestrial deposits of Europe can be correlated with marine beds and hence placed in the appropriate stage. But in North America this is not so readily done, for most American mammalian deposits are in the interior western states, far from marine fossil-bearing sediments. A series of ages based on the mammals contained in the various North American beds has, however, been established, and approximate correlations can be made between these ages and the European ones. A similar series has been erected for South American deposits. These three series of ages are given in Table 4, together with data on the best-known localities, areas, or formations in the various continental areas.

Cenozoic deposits.—The best and most complete series of mammal-bearing beds is that found in western North America, where sediments, spreading out from the Rocky Mountains and Sierras, have preserved a good record of numerous faunas ranging from the beginning of the Cenozoic to the Pliocene. Europe in Tertiary times was a peninsular area frequently flooded by shallow marine waters; the deposits along the shores of these seas or derived from the rising Alps include numerous fossiliferous formations which have been studied intensively for more than a century. In Asia early Tertiary deposits are well represented in Mongolia; later epochs are best represented in the Siwalik Hills and other areas of sediments from the rising Himalayas; Burma supplies further data for the early Tertiary and Pleistocene, China for the later Cenozoic, Java for the Pleistocene. In Australia, Pleistocene fossils are rather plentiful, but only a single terrestrial mammal is known from the entire Tertiary. Africa appears to have been a stable land mass during most of the Cenozoic; apart from later Eocene and early Oligocene faunas from Egypt, Tertiary continental deposits are extremely restricted in area and faunas. In South America there are extensive sediments in Patagonia, which have preserved much of the curious fauna of mammals which evolved there during Tertiary times.

Cenozoic conditions.—We have little reason to believe that there has been much alteration in the extent or position of the continental areas during the Cenozoic, and almost all known facts in the distribution of mammals may be accounted for by small changes in the present continental relations. It is probable that Australia has been in its present condition of isolation since the end of the Mesozoic, for almost none of the Cenozoic types of terrestrial mammals has reached that region. The independent evolution seen in South American mammals indicates that that continent became separated from North America very early in the Cenozoic and that an easily traversed connection was not rebuilt until about the end of Tertiary times. Although, as noted above, the history of Tertiary Africa is poorly known, it is very probable that this region was isolated from Eurasia during the earliest Cenozoic and that opportunity was given there for the initiation of peculiar and characteristic placental groups. Comparison of successive North American and Eurasian faunas indicates that the Bering Straits connection between the two areas was made and broken a number of times.

Various Tertiary land bridges have been proposed between continental areas to account for real or fancied similarities between the regions so connected. Most of them rest on flimsy evidence and need not be considered here. Stronger support has been given to a proposed connection between South America and Australia, either directly or via Antarctica. This is based upon the similarity in the marsupials of the two continents; but this similarity can be as readily explained as being due to parallel evolution from common ancestors, which were presumably widespread in northern continents in late Mesozoic days. The most serious problem, discussed earlier, is that regarding a Tertiary bridge between South America and Africa.

Early Tertiary times seem to have had an equable, warm climate, which gradually gave place to the extreme temperature differences found in the Ice Age, with a cold arctic zone grading rapidly southward into warm tropics, a situation still existing at the present time. This climatic change seems to have resulted in a slow southward retreat of many forms from the better-known regions of Eurasia and North America and the survival in the tropics of many groups long after their extinction in the present north-temperate zone. The peccaries and tapirs of South America are relatively recent migrants from the north; the antelopes and associated mammals of tropical Africa form a fauna strikingly similar to that of Europe in the early Pliocene.

The geographic regions customarily used by zoögeographers in interpreting the distribution of life today reflect accurately the geological history. Some six regions are generally accepted: the Palaearctic, for Europe and the Mediterranean region and northern and central Asia; Nearctic, for North America; Oriental, for southern Asia and the East Indies; Ethiopian, including most of Africa; Neotropical, for South and Central America; and Australian, including Australia, New Guinea, and certain adjacent islands.

These six regions are not all equally distinct from one another. The Australian region stands in sharp contrast with all five other regions in its faunal content, a feature associated with the separate Cenozoic history of that continent. The Neotropical region also shows very individual characteristics, due to the development of a peculiar fauna during the Tertiary isolation of South America. The Palaearctic and Nearctic regions are identical in climate and separated only by the variable make-and-break between Alaska and Siberia. Their faunas are so similar that they are frequently considered as a single Holarctic area. The distinction of Ethiopian and Oriental regions from the Palaearctic is due primarily to the relatively recent establishment of sharp temperature gradients; during much of the Tertiary the three were essentially a single faunal unit.

The major interest in the Cenozoic lies in mammalian history; in most of the other vertebrate groups relatively little evolution took place during this era, and a treatment of them by successive epochs is unnecessary.

Fishes.—Shark and ray teeth are common in many Tertiary marine beds, and chimaeroid toothplates are occasionally present; only in exceptionally favorable circumstances are skeletons of cartilaginous fishes discovered. All, or nearly all, existing groups of sharks, skates, and rays appear to have been established in the early Tertiary, and but little further evolution appears to have taken place. Actinopterygians below the teleost level are rare in the Cenozoic. The pycnodonts persisted into the Eocene; today there survive only the African polypterids, the sturgeons, paddlefishes, garpike (*Lepidosteus*), and *Amia*, the bowfin. The last three are represented by characteristic specimens from the Eocene, the first two by fragmentary remains of equally early date. A single living coelacanth crossopterygian has been recently discovered; but no Tertiary fossils are known, presumably because this group had taken up life in the deep seas, an environment of which there are few known geological records. Of the three surviving lungfishes, there are Tertiary records of the Australian and African genera but not of the South American form.

The teleosts are the dominant Tertiary fishes and are found in a variety of deposits both fresh and salt in origin; the shales of the Green River region of North America and of Monte Bolca in Italy are famous Eocene fish localities; diatom beds in California and marine deposits in Algeria and at Licata in Sicily are among prominent late Tertiary deposits. In fresh waters the dominance of the Ostariophysi, the carp-catfish group, is a striking feature of the Cenozoic; in marine deposits there is an increasing variety of higher, spiny-finned teleosts, although the old-fashioned isospondyls are still abundant.

Amphibians and reptiles.—Amphibian remains are relatively rare in the Tertiary and shed little light on the history of the frog and salamander groups represented. Turtles are abundant in many formations, and most of the living types are already represented by close relatives at the very beginning of the era. In the Eocene the primitive amphichelydians became extinct. The pleurodires, subsequently rare as fossils, have been confined to the southern continents since the earlier Cenozoic. Lizards are not infrequently discovered. The snakes are the one progressive group of reptiles during these latter times; poisonous snakes are apparently a Tertiary reptilian innovation. Crocodiles, mostly related to living forms, are fairly numerous throughout the period. *Champsosaurus* of the late Cretaceous persists into the early Eocene. Fossil representatives of the typical Rhynchocephalia are unknown.

Birds.—It has been said that the Cenozoic is as much the Age of Birds as it is the Age of Mammals; the birds are the dominant group in the air during the entire era. The fragile nature of their bones and their usually small size have rendered the unraveling of their history difficult. The principal points in their Tertiary history, including the sporadic development of large flightless forms, have been noted in an early chapter. Toothed forms appear to have become extinct by the end of the Cretaceous; except for some tropical types, almost every large group of modern birds, and even most of the major families, were already present in the early Tertiary.

PALEOCENE

This oldest of Tertiary epochs is relatively poorly represented in the marine sequence, but the existence of a pre-Eocene chapter is abundantly proved by numerous older continental deposits, particularly well developed in North America. In the San Juan basin of New Mexico and southern Colorado, Lower, Middle, and Upper Paleocene deposits are represented by the Puerco, Torrejon, and Tiffany beds; the Polecat Bench formation of northwestern Wyoming appears to cover the entire time interval between the end of the Cretaceous and the true Eocene; "Fort Union" beds in eastern Montana and adjacent states have produced Paleocene mammals in various areas, particularly in Middle Paleocene deposits near the Crazy Mountains; the Dragon fauna of Utah is an early Middle Paleocene assemblage.

In other continents Paleocene mammals are unknown, rare, or of late date. In Australia, as we have noted, the Paleocene fauna is unknown, as is that of the later Tertiary eras; and there are no African Paleocene mammals. In Europe there are a few late Paleocene forms mainly from Cernay near Rheims; in Asia a small assemblage, apparently equally late in time, is found in the Gashato of Mongolia. In South America a handful of specimens has recently been discovered in the Rio Chico of Patagonia, some of which come from an obviously late horizon; a few scraps may be earlier. In consequence, our discussion of the Paleocene is based mainly on the American record as seen in the Puerco and Torrejon and their equivalents; the late American Paleocene and that of other continents is considered separately.

The terrestrial fauna of the Paleocene, with the dinosaurs absent, is mainly a mammalian one. But if we were able to visit the Paleocene, the aspect of the fauna would be of a strange and unfamiliar sort. Many of the mammals then present are assigned to orders still existing—Insectivora, Carnivora, Primates—but these Paleocene representatives of the modern orders were for the most part archaic or aberrant types. Not a single living family is present in the characteristic Paleocene, and much of the fauna belonged to orders now entirely extinct.

The few mammalian types known in the Cretaceous are still present. Opossum-like marsupials persist in insignificant numbers. The archaic multituberculates, on the other hand, are present in abundance; most were small members of the *Ptilodus* group; but, in addition, we find *Taeniolabis* and its allies, forms of considerable size and still higher specialization.

The insectivore types persist from the Cretaceous into the Paleocene but are not particularly prominent; once having played its part as ancestral placentals, this order is tending to sink into the relatively insignificant role it plays today. There are a few zalambdodonts and a number of genera of the leptictids, forms leading toward the dilambdodont families of later epochs. Rather more prominent are some side branches, such as *Mixodectes* and the pantolestids, which had departed far from the typical insectivores but were hardly important enough to merit ordinal separation.

Much more prominent were early carnivores, represented by a score of genera. Almost all are members of the Acreodi, without specialized carnassials and still very close to their insectivore ancestors; from them by the Middle Paleocene had developed *Dissacus* and other early members of the blunt-toothed mesonychids. The pseudocreodonts, characteristic of the

Eocene, are not present in typical Paleocene horizons, but the progressive miacids, destined to give rise to modern carnivores, were represented, although sparsely.

A third placental group is that of the primates, which appear in the Middle Paleocene. The forms present are more or less transitional in their cheek teeth between the insectivores, on the one hand, and lemurs and tarsioids, on the other. A puzzling feature is that nearly all the Paleocene genera, in several different families, have developed large and often rodent-like incisors, perhaps in relation to some type of feeding habit now difficult to interpret.

Ungulates were abundant, but ungulates of unfamiliar types, of primitive structure, and, for the most part, of small size. Almost all may be included in the Condylarthra as a basal order of hoofed mammals. The low-crowned, "squared-up" molars indicate a shift to a herbivorous diet; hoofs are present in some cases, but not all; in many respects, however, the early condylarths were still close to the insectivore-carnivore stock. Four families are present, of which *Mioclaenus*, *Periptychus*, *Meniscotherium*, and *Tetraclaenodon* are representative. The first three are apparently rather aberrant; the last is a member of the phenacodont family which may be close to the ancestry of more advanced ungulate orders.

The orders so far mentioned are still so close to the ancestral placentals that the group boundaries are difficult to determine; were we ignorant of their later histories, we should be justified in including almost the entire assemblage in a single ordinal group.

More divergent forms were, however, already making their appearance. The distinction is often made between "archaic" and "progressive" mammal groups, the former being types which tended to a high degree of specialization at an early stage but were destined for early extinction; the latter, forms which tended to evolve more slowly but with greater adaptability and greater success. Among the earlier Paleocene mammals, archaic types are already distinguishable in the taeniodonts, such as *Conoryctes*, the giants of their times, and *Pantolambda*, an ungulate which had already grown to the size of a sheep and which in its relatively heavy build foreshadows the larger amblypods of later times. A tendency toward prematurely large size is also seen in some of the condylarths and certain of the carnivores.

Following the typical faunas of the epoch, we find in the late Paleocene of North America a fauna in which most of the groups previously present still persist but are often represented by larger types and in which the mammalian assemblage is more varied and foreshadows that of the true Eocene. The Acreodi are already reduced in numbers, and the presence of *Oxyaena* marks the appearance of the Pseudocreodi. The early ungulates were increasing in size and variety; particularly prominent were great amblypods, such as *Barylambda* and, at the end of the Paleocene, *Coryphodon*. Several new mammalian groups appear, however, whose earlier history is unknown. These in-

TABLE 4

CENOZOIC VERTEBRATE LOCALITIES

Epoch	European Ages	European Localities	Asiatic Localities	African Localities	North American Ages	North American Localities	South American Ages	South American Localities
Pleistocene		Caves, river terraces, etc., early Pleistocene inc. Villafranchian of Val d'Arno (Italy), Perrier (France), Norwich Crag (Eng.)	Pinjor (Siwaliks); fissure deposits of Sze-Chuan and loess of China; Irrawaddy beds (Burma); volcanic ash deposits of Java	Caves and superficial deposits in Algeria, E. Af. (Oldoway, etc.), S.Af.		Caves, postglacial bogs; La Brea, McKittrick (Calif.); Hay Springs, Broadwater (Neb.)		Pampean beds (Arg., etc.) Tarija (Bolivia); Brazilian caves
Pliocene	**Astian**	Roussillon, Montpellier (France)	Dhok Pathan (Siwaliks)		Blancan	Hagerman (Idaho); Benson, San Pedro (Ariz.); Rex Road (Kan.); Blanco (Tex.)	Chapadmalalan	Chapadmalal fauna of Pampas
	Plaisancian	Perpignan, Trévoux (France); Red Crag (Eng.); Piemont region (Italy) _M_*	Nagri (Siwaliks)		Hemphillian	Rattlesnake (Ore.); Hemphill (Tex.); Long Island (Kan.); Ash Hollow (Neb.)	Monteher-mosan, Tunuyanian	Tunuyan beds and part of Araucanian series (W. Arg.); Monte Hermoso (southern Pampas)
	Pontian	Concud (Spain); Curcuron, Mt. Léberon (France); Antwerp (Belg.) _M_; Eppelsheim (Ger.); Vienna basin (Austria) _M_ (in part); Pikermi, Samos (Greece)	Maragha (Persia); Chinji (Siwaliks); Honan, Shansi, red beds (China)	Wadi Natrûn (Egypt)	Clarendonian	Santa Fe, in part (N.M.); Clarendon (Tex.); Snake Creek, in part, Burge (Neb.)	Huayquerian, Mesopotamian	Huayqueria beds and part of Araucanian series (W. Arg.); Mesopotamian beds (Entre Ríos region, Arg.)
Miocene	**Sarmatian**	Antwerp (Belg.) _M_; Sevastopol (Russia)	Kamlial (Siwaliks); Tung Gur (Mongolia)	Moghara (Egypt) Uganda	Barstovian	Pawnee Creek (Colo.); Madison Valley (Mont.); Mascall (Ore.); Barstow, (Calif.)	Chasicoan, Friasian	Chasico beds (of southern Pampas); Rio Frias beds (of western Patagonia)
	Vindobonian	Sansan, Simorre, Grive St. Alban, St. Gaudens (France); Eibiswald, Eggenburg, etc. (Austria); Molasse of central Europe in part; Steinheim, Oeningen (Ger.), Mte. Bamboli (Italy); Belg. _M_	Loh (Mongolia)		Hemingfordian	Sheep Creek, Marsland (Neb.); Hawthorn (Fla.); Temblor (Calif.); Calvert (Md.) _M_	Santacrucian	Santa Cruz beds of Patagonia
	Burdigalian, Aquitanian	Faluns of Touraine, St. Gérand-le-Puy, Agen region, Orléans sands (France); Molasse of central Europe in part; Mainz basin, Ulm (Ger.)	Bugti beds (Baluchistan)	Kenya Colony; Namib (S.W.Af.)	Arikareean	Gering, Monroe Creek, Lower Harrison (Neb.); Rosebud (S. D.); M.-U. John Day (Ore.)	Patagonian	Patagonian formation _M_

* _M_ = marine.

TABLE 4—*Continued*

Epoch	European Ages	European Localities	Asiatic Localities	African Localities	North American Ages	North American Localities	South American Ages	South American Localities
Oligocene	**Chattian**	**Sandstones of Beauce *M*, La Rochette, La Milloque, Agen region (France); Mainz basin (Ger.); Cadibona (Italy)**	Hsanda Gol (Mongolia) Turgai Turkestan)		Whitneyan	Upper Brulé (*Protoceras* beds) of White River series (S.D., N.D., Neb., Wyo., Colo.)	Colhuehuapian	Colhué Huapí beds (*Colpodon* fauna) of Patagonia
	Stampian (Rupelian)	**La Ferte-Aleps, Bournoncle-St. Pierre, Aveyron, Quercy phosphorites in part (France); Flonheim, Weinheim (Ger.)**			Orellan	Lower Brulé (*Oreodon* beds) of White River series (S.D., N.D., Neb., Wyo., Colo.)		
	Sannoisian (Lattorfian)	**Quercy phosphorites in part, Ronzon, Brie limestone, Lobsann (France); Hampstead beds (Eng.)**	Ulan Gochu Mongolia)	Upper beds of Fayûm (Egypt)	Chadronian	Chadron (Titanothere beds) of White River series (S.D., N.D., Neb., Wyo., Colo.)	Deseadan	Deseado beds (*Pyrotherium* fauna) of Patagonia
Eocene	**Ludian, Bartonian**	**Gypsum beds of Montmartre, Quercy phosphorites in part, Débruge, Gargas, St. Hippolyte de Caton, Robiac, Castres, Calcaire de St. Ouen (France); Mormont (Switz.); Isle of Wight (Eng.)**	Ardyn Obo, Shara Marum, Irdin Manha (Mongolia); Pondaung (Burma)	Qasr-el-Sagha beds of Fayûm, Upper Mokattam beds *M* (Egypt)	Duchesnean, Uintan	Duchesne River, Uinta (Utah); Washakie in part (Wyo.); Sespe in part (Calif.); Jackson of southeastern states *M*		
	Auversian, Lutetian	**Calcaire grossier, Issel, Argenton, Buchsweiler (France); Bracklesham (Eng.); Egerkingen (Switz.); Mte. Bolca (Italy)**		Mokattam beds *M*., Birket-el-Qurûn (Egypt); Nigeria *M*	Bridgerian	Bridger, Washakie in part (Wyo.); Green River in part (Wyo., Colo., Utah); Huerfano in part (Colo.)	Mustersan	Musters beds with ***Astraponotus*** fauna (Patagonia)
	Cuisian, Sparnacian	**Argile plastique of Soissons region, Meudon, Epernay (France); London clay (Eng.); Erquelines, Orsmael (Belg.)**			Wasatchian	Largo, Almagre (N.M., Colo.); Huerfano in part (Colo.); Gray Bull of Bighorn basin, Lysite and Lost Cabin of Wind River basin (Wyo.)	Casamayoran	Casa Mayor beds with ***Notostylops*** fauna (Patagonia)
Paleocene	**Thanetian**	**Cernay (France); Thanet sands *M* (Eng.)**	Gashato (Mongolia)		Clarkforkian, Tiffanian	Clark Fork, Silver Coulee, Polecat Bench in part (Wyo.); Fort Union in part (Wyo., Mont.); Plateau Valley (Colo.); Tiffany (N.M.); Paskapoo (Alberta)	Riochican	Rio Chico (Patagonia); Pernambuco *M* (Brazil)
	Montian				Torrejonian, Dragonian	Torrejon (N.M.); Polecat Bench in part (Wyo.); Crazy Mountain Field, Fort Union (Mont.); Dragon fauna (Utah)		
					Puercan	Puerco (N.M.); Polecat Bench in part (Wyo.)		

clude the first of the uintatheres among archaic ungulates; the first of the peculiar tillodonts; *Palaeanodon*, an ancient relative of the South American edentates; and *Paramys*, an ancestral rodent.

The few Paleocene mammals of Europe, late in date, add little to our knowledge of mammalian evolution. Such forms as have been discovered appear to be close to American mammals of similar age, although generically distinct, and indicate that there was a common fauna widespread in northern regions. The known Paleocene of Asia, equally late in date, is puzzling and disappointing. It was long believed that Asiatic beds of this age, when discovered, would reveal the ancestors of some of the groups, particularly of "modern" orders of ungulates, absent in the American Paleocene. The single fauna so far found, the Gashato, has not realized these hopes. It reveals, much as in North American beds of the same horizon, multituberculates, insectivores, carnivores, and condylarths and a uintathere. A welcome find is the oldest fossil hare, *Eurymylus*. The commonest fossil is an ungulate, *Palaeostylops;* but, startlingly, this belongs not to any normal northern group but to the characteristic South American order of Notoungulata.

In South America itself the Rio Chico beds appear to be Paleocene. A few fragments may come from fairly low levels; most, however, appear to be late in date. The material is poor but shows, nevertheless, that most of the groups which were to characterize the later Tertiary of that continent were already present. These forms include marsupials, edentates (represented by armadillo scales), litopterns, condylarths presumably related to litoptern ancestry, notoungulates, and possibly astrapotheres and pyrotheres. We are accustomed to think of the Northern Hemisphere as the area of origin of mammalian groups and hence tend to interpret the presence of these forms as due to early migration from the north. It is, however, equally possible that part or all of the distinctive South American mammals had developed locally.

It is obvious that our known Paleocene faunas, while giving us interesting chapters in the early deployment of the placentals, do not give us a complete story. As we have said, neither the Paleocene nor any other Tertiary epoch gives us any idea of marsupial evolution in Australia. There are no Paleocene deposits in Africa, where one may expect that the early development of subungulates and possibly other types was under way.

We have, further, no knowledge of stages in the evolution of rodents and lagomorphs, which appear fully developed at the close of the Paleocene, or of the perissodactyls and artiodactyls, which appear abruptly at the beginning of the Eocene. Possibly these orders may have been evolved in some area of Eurasia or North America unrepresented in our present records; possibly in familiar regions but in environments not represented by fossiliferous deposits.

EOCENE

In the Eocene, North America is, again, the continent in which the faunal sequence is most abundantly represented. Lower Eocene faunas, usually termed "Wasatch," are present in abundance in the Bighorn and Wind River basins in Wyoming; the Bridger basin of southwestern Wyoming is the classic Middle Eocene collecting ground; that for the Upper Eocene is to the south in the Uinta basin of northeastern Utah.

In Europe the Lower Eocene is known from relatively poor beds in the London basin and in related deposits in northern France and Belgium; later Eocene horizons are increasingly fossiliferous, including such well-known localities as Egerkingen in the Swiss Middle Eocene and the Upper Eocene gypsum beds of Montmartre (Paris). The Quercy phosphorites of south-central France are cave fillings in older limestones containing numerous small mammals. Part are late Eocene; the later deposits extend into the Oligocene. In Asia there are few fossils before the latter part of the epoch, when several faunas are present in Mongolia and in Burma. In South America the Casa Mayor beds are probably of early Eocene age; the Musters, also in Patagonia, rather later. Africa now enters the Tertiary terrestrial record. The Mokattam beds of Egypt contain a marine mammalian fauna of Middle Eocene age, and continental deposits begin in the Fayûm of western Egypt in late Eocene times.

In the Lower Eocene, it appears, the northern continental areas formed, much as today, a single zoögeographic region, for Europe and North America had many genera in common. There was no sharp break between the life of the Paleocene and the new epoch; for, with the exception of the *Periptychus* type of condylarths, every major group present here in the Paleocene was still present. Most of the older groups were destined to become extinct; but their disappearance was a gradual one. The earliest Eocene contains the last survivors of the long-lived multituberculates; opossums (*Peratherium*) persist from the Eocene onward into the Miocene of both Europe and North America. There are insectivores—primitive, typical, and aberrant. Creodonts dominate the scene among carnivores. The Acreodi, however, were rapidly replaced by numerous pseudocreodonts of the oxyaenid and hyaenodont families, with well-developed carnassials. The aberrant primates of the Paleocene are still present and, in addition, more typical lemurs, such as *Notharctus*. Condylarths persisted in the Eocene, where *Phenacodus* is a familiar Lower Eocene ungulate and *Hyopsodus*, a late survivor, represented the group in America until the end of the epoch. *Paramys* and other rodents are present in both continents, but the order is relatively rare in the earlier European Eocene. The amblypod *Coryphodon* is found in the Lower Eocene in Europe and America alike. A second curious appearance of the notoungulates (in addition to *Palaeostylops*) is that of a single fragment from the Lower Eocene of Wyoming; except for these occurrences, notoungulates have never been reported beyond the confines of South America. Uintatheres were never present in Europe but developed further in North America. The tillodont *Esthonyx* was present in both hemispheres; taeniodonts were present in the American Lower Eocene but not in Europe.

The diagnostic feature marking the beginning of the Eocene is the presence of the two great modern groups of ungulates—the perissodactyls and the artiodactyls. Both appear simultaneously and seemingly abruptly in Europe and North America in Lower Eocene times. In both groups the ordinal characters are fully established, but their ancestry and areas of development are unknown. In the early Eocene the artiodactyls are rare. The perissodactyls, on the other hand, were at once abundant; *Eohippus* and primitive tapiroids are common finds in the "Wasatch," and close relatives were present in Europe; in North America the first titanotheres and chalicotheres were present before the close of the Lower Eocene.

For the later history of the Eocene in the Holarctic area, Asiatic evidence is available, as well as that from the European and American extremities of the region. In some groups the entire area shows a fairly uniform picture, in others—notably the ungulates—there are marked differences which suggest regional isolation in the Middle Eocene, partially corrected by intermigration toward the end of the epoch.

Bats appear full-fledged in both hemispheres in the Middle Eocene; various primitive and aberrant primates persisted throughout the epoch. Among the carnivores, typical acreodonts became extinct early in the Eocene, but other creodonts flourished in all three northern areas. The Pseudocreodi are the characteristic carnivores; some remained small but others, such as *Pterodon* and *Hyaenodon* of both hemispheres and the oxyaenid *Sarkastodon* of Mongolia, tended to grow to great size. The blunt-toothed mesonychids are absent in Europe after the early Eocene but remained until the end of the epoch in North America and Asia, *Andrewsarchus* of the latter continent being a giant form. Miacids are common in both land masses. In the late Eocene this family comes to an end, seemingly by the evolution from it of the first of the more typical fissipedes, with such forms as *Cynodictis* and *Procynodictis* representing the forerunners of civet, weasel, dog, and cat families. Primitive aplodontoid rodents are present in both hemispheres but are more common in North America, where rodent families of this group continued to flourish in the later Tertiary. We have noted the occurrence of a rare lagomorph in the Paleocene; the next record of hares is in the Upper Eocene of eastern Asia and North America; the former continent may well have been the place of their development.

Many features in the history of nonungulate mammals in the later Eocene are thus similar in Eurasia and North America. But there were notable differences; the former region shows, on the whole, the more progressive situation. Shrews and moles are present in Europe by the end of the Eocene but do not appear in North America until later; on the other hand, the aberrant mixodectid insectivores persisted in North America in the later Eocene, as did the taeniodont *Stylinodon*, tillodonts, and palaeanodont edentates. Among the rodents the pocket gophers appeared in the late Eocene in North America; in Europe there developed at this time anomaluroid families possibly ancestral to hystricoids and myomorphs.

It is among the ungulates that Europe and North America show the greatest divergences in the course of the Eocene. Most of the archaic ungulates of the Paleocene and early Eocene have become extinct in both areas. In North America, however, the ungainly uintatheres and the small condylarth, *Hyopsodus*, survived until the end of the epoch. Perissodactyls flourished in both regions but followed different lines of development in many respects. In North America the horses, in the form of the relatively rare genera, *Orohippus* and *Epihippus*, remained conservative in size and structure; in Europe, on the other hand, there was a rapid trend toward large size and specialization, some specimens of the three-toed *Palaeotherium* of the late Eocene being even larger than modern horses. Primitive tapiroids were present in both continents but more abundant in Europe, where *Lophiodon* was a typical large form. Primitive running rhinoceroses are absent in the European Eocene; *Hyrachyus* and its relatives are confined to North America. More progressive running rhinoceroses—the hyracodonts—and such amphibious forms as *Amynodon* inhabited both North America and Asia. In the late Eocene of all three northern continents are found the first rare specimens of the true rhinoceroses which were to become abundant in the Oligocene. The oldest recorded chalicothere is from the Middle Eocene of North America; but by the late Eocene this family is represented in the Asiatic area in which it later flourished. Titanotheres, too, are first found in North America but by the end of the epoch were developing vigorously in Asia as well, and two stragglers have been discovered in eastern Europe.

Still more divergent in development were the artiodactyls, which, we have noted, were rare in early Eocene days. Little progress appears to have taken place in the group in North America. In Europe and Asia, however, middle and late Eocene faunas show a remarkable expansion. Some of the types developed were bunodonts suggestive of later pigs and peccaries, although apparently not the actual ancestors of these forms. Most, however, are primitive selenodonts—caenotheres, anoplotheres, and xiphodonts are the dominant European types. In the late Eocene of that continent are found, further, primitive pecorans, in such forms as *Amphimeryx* and the tragulid *Gelocus*. In the Upper Eocene there appears in North America, apparently as the result of invasion from Asia, a similar series of artiodactyls, which, however, belong to different families. They include some rather piglike types, primitive selenodonts ancestral to the camels, oreodonts and agriochoeres, and a considerable number of pecorans of the distinctive hypertragulid group.

We have noted above some features in which the later Eocene of Asia is comparable faunally with Europe or North America or both. Imperfect, however, as our knowledge of Eocene history there is, we can see that in certain respects Asia had developed differently from the regions to west or east. Among the primitive ungulates, large condylarths and uintatheres persisted there through the Eocene. Horses were absent, but tapiroids were apparently common. Anthracotheres were very abundant in the late Eocene and may have developed in that area. *Archaeomeryx* of Asia is the most primitive known hypertragulid; presumably this group reached America from an earlier Asiatic home, and quite probably the camels and oreodonts were of Asiatic origin.

In the middle and later Eocene appear the first representatives of the two purely marine orders of mammals, the Cetacea and the Sirenia. We are ignorant of their terrestrial forebears and cannot be sure of their place of origin. But although archaeocete whales (such as *Basilosaurus*) and sirenians are found in the American Eocene, most of the earliest and most primitive types are from the Mediterranean region and especially from the Mokattam beds of Egypt. This suggests that these groups originated in Africa during the earliest Tertiary. The only known terrestrial African mammals of the Eocene are the early proboscideans *Moeritherium* and *Barytherium* from the Fayûm. Not improbably, proboscideans, sirenians, and hyracoids (which appear slightly later in that area) are products of early Tertiary African evolution from a primitive subungulate stock.

In South America the Casa Mayor beds of the early Eocene give us our first adequate picture of the specialized Tertiary faunas of that continent; the Musters beds of the Middle Eocene show a slightly more advanced stage. Except for rodents and primates, all members of the Tertiary assemblage are represented. Marsupials were abundant and include not only opossums but larger and more strictly carnivorous borhyaenids (one already as large as a wolf), caenolestids, and *Polydolops* and its relatives which paralleled the multituberculates in dentition. Edentates are represented by armadillos of a primitive nature, such as *Utaetus*. *Didolodus* and similar types are currently regarded as condylarths related to the ancestry of the litopterns; of these latter there are genera ancestral to the two families prominent in the later Tertiary. The Notoungulata are, as later, the commonest of ungulates; the Eocene genera appear to include forms antecedent to the various subgroups of later epochs as well as numerous primitive notioprogonians such as *Notostylops;* all are small, primitive, little differentiated, and with low-crowned teeth. The astrapotheres and pyrotheres, as archaic ungulates, appear to have played in South America the role of amblypods and uintatheres of the Northern Hemisphere; large representatives of these two groups were the giants of the fauna.

OLIGOCENE

European Oligocene deposits are numerous. A portion of the Quercy phosphorites are of early Oligocene date. Ronzon in France and the Mainz basin in Germany are among the better-known localities, a large proportion of which are located in France. In Asia, Oligocene continental beds are almost entirely confined to Mongolia, with Ulan Gochu and Hsanda Gol as the main sites. The earliest of important Tertiary terrestrial African deposits is that of the Lower Oligocene of the Egyptian Fayûm. In North America the main fossil localities are those in the White River series in South Dakota and adjacent states, with successive titanothere (Chadron) and *Oreodon* and *Protoceras* beds (Brulé). In South America, Patagonia continues to be the exclusive area of interest. The Deseado beds, with the *Pyrotherium* fauna, are Lower Oligocene; the late Oligocene Colhué Huapi beds contain essentially a Miocene assemblage.

In the northern continents the Oligocene fauna has a much more modern appearance than that of the Eocene. This is not due in any measure to the appearance of new types; for hardly a third of the living families of terrestrial mammals were then present and, except in the case of the carnivores, there were few new groups introduced at this time. This more modern aspect is rather due to the extinction, during or at the close of the Eocene, of a great number of families and even orders which were characteristic of Paleocene and early Eocene days. To cite this list is to cite the greater part of the roster of the typical Paleocene mammals, including multituberculates, primitive insectivore groups, arctocyonid creodonts, miacids, condylarths, and plesiadapid primates and, in addition, a number of the late Paleocene and Eocene families, such as mesonychid and oxyaenid creodonts, adapid lemurs, and a few of the more primitive forms among the modern ungulate orders.

In the Holarctic land areas, there continues, in the Oligocene, the faunal situation established in the later Eocene, with geographical continuity in some groups (particularly in some of the carnivores) and independent parallel evolution in others, notably the ungulates. Europe and North America offer two extremes; Asia has characteristics of both, although showing greater affinities with Europe. There are few features suggesting any great interchange of faunal elements between the two hemispheres during the Oligocene; most of the common characteristics appear to have resulted from a late Eocene interchange.

Common types include such forms as oppossums, the major families of modern insectivores, and primitive beavers, which appear in the late Oligocene. In both hemispheres there appear in the Oligocene the first representatives of the great murid group, destined to play an increasingly important role in the later epochs. Among carnivores both hemispheres show the persistence in the early Oligocene of the last surviving group of the creodonts, in *Hyaenodon* and its relatives, later confined to tropical regions. A new development of importance is the rapid deployment of progressive fissipede families developed from the miacids. Canids of various types, mustelids, and felids, both saber-tooths and false saber-tooths of the *Dinictis* group, were abundant in both hemispheres.

A limited number of ungulates are common to both hemispheres. Among the perissodactyls, chalicotheres were present in Eurasia and doubtfully in North America; *Protapirus*, first of true tapirs, also appears in both areas; amynodont rhinoceroses are widespread, with *Cadurcotherium* as European representative, *Metamynodon* the American genus. A notable perissodactyl development is the expansion of the true rhinoceroses during the Oligocene in such primitive genera as *Caenopus* in North America and *Aceratherium* in Eurasia. Among the piglike artiodactyls there are common bunodont families. *Anthracotherium* and other members of its family are abundant in Eurasia, and *Bothriodon* penetrated to America, where the group failed to survive. Pigs and peccaries make their appearance; both are found in Europe, and the peccaries reached their later American center in the Oligocene.

Among the nonungulates the Eurasian Oligocene reveals various groups absent from America; the first of viverrid carnivores, a group which never reached the Americas; ochotonids, which arrived there much later; anomaluroid rodents, the first dormice and dipodoids, and forms which may be the first bathyergoids. Among the perissodactyls the only distinctive European forms are *Palaeotherium* and its relatives, which persisted until the Middle Oligocene. There were, however, numerous selenodont artiodactyls peculiar to Eurasia. *Dichobune, Caenotherium, Anoplotherium,* and *Xiphodon* are examples of archaic forms "held over" from the Eocene and for the most part exterminated before the close of the epoch. More important, however, were primitive pecorans, such as *Amphimeryx* of the early Oligocene, and tragulids, such as *Gelocus* and *Bachitherium*.

North America shows equally distinctive features. There are various rare hold-overs here of the archaic Paleocene and Eocene groups—the last anaptomorphid and apatemyid primates, leptictid insectivores, palaeanodont edentates; surviving ischyromyid rodents, and their derivatives, such as the mylagaulids and ancestral sewellels; ancestors of the pocket gophers and kangaroo rats; hares, present here and in Asia but not as yet in Europe.

Among ungulates, the perissodactyls are more prominent in North America than in Oligocene Europe. Small three-toed horses, *Mesohippus* and *Miohippus*, flourished; *Hyracodon* is a common rhinocerotoid; primitive tapiroids survived; the lowest Oligocene beds are characterized by the presence of numerous giant titanotheres, which disappeared abruptly before the Middle Oligocene. Artiodactyls are increasingly important, however. Camels, such as *Poëbrotherium*, are common; *Protoceras* represents a peculiar American family of primitive pecorans; *Leptomeryx* and other hypertragulids are common Oligocene finds; *Agriochoerus* is present. The oreodonts become in the Oligocene the commonest of ungulates; *Oreodon* and other members of the family are the most frequent fossil finds in middle and late Oligocene deposits.

Known Asiatic deposits show that many of the European Oligocene groups were represented in that continent, and accidents of preservation and collection may be responsible for the seeming absence of other European families. Distinctive Asiatic features include the absence of equoids of any sort, with a variety of surviving tapiroids in their place; the presence of a last lingering amblypod; the development of giant rhinoceroses, such as *Baluchitherium*, which persisted until the Miocene. Other features, implying a connection with North America in the late Eocene or early Oligocene, include the common presence of hares and of abundant giant titanotheres.

We have noted the almost complete lack of Paleocene or Eocene African terrestrial records. In the Lower Oligocene we at last find an African fauna; this, unfortunately, lies at the northern margin of the continent, in the Egyptian Fayûm, and shows evidences of invasion from Eurasia. In the known fauna there are no fissipedes, but hyaenodont creodonts such as *Pterodon* and *Hyaenodon;* a considerable variety of anthracotheres; *Phiomys*, representing the anomaluroid rodents destined to survive into the African Miocene. All these forms may be recent immigrants, since they are members of contemporary Eurasian families. More doubtful as to origin are anthropoid primates, unknown earlier (except for possible Burmese forms). These include a very primitive anthropoid, *Parapithecus;* in *Apidium* a true Old World monkey; in *Propliopithecus* an early, manlike ape. Definitely autochthonous forms are represented by *Arsinoitherium;* a considerable variety of hyracoids; and proboscideans, which now include not only the archaic *Moeritherium* but the mastodonts, *Palaeomastodon* and *Phiomia.*

The Deseado beds of Patagonia show an important phase in the development of the isolated South American fauna. Except for marsupials of the *Polydolops* type and a few families of ungulates, all Eocene groups are still present. Marsupial carnivores are numerous and varied (one was larger than a cave bear). Edentates were still rare but were increasing in variety, for glyptodonts had appeared in the late Eocene and ground sloths of modest size had also made their appearance. The native ungulates had already reached a climax in size and variety. Both major families of litopterns were advanced in their development. Notoungulates were numerous and exceedingly varied; high-crowned teeth had developed in many lines. Most characteristic of the notoungulates of the age were *Leontinia* and large related types. Huge astrapotheres were present, and the giant of the fauna was the elephant-like *Pyrotherium*.

A startling phenomenon is the abrupt appearance of hystricoid rodents. There is no trace of rodents in the Eocene of the continent, and it is highly improbable that these forms, so successful from this time on, could have been present earlier and escaped discovery. As we have noted in an earlier chapter, an African origin seems probable, but their means of transport offers a difficult problem.

Oligocene marine mammals are rare, perhaps because of the rarity of appropriate types of sediments. Sirenians are known from the European Oligocene. An archaeocete whale is known to have survived, and we are sure that the differentiation of more modern whale groups was well advanced, for a lone squalodont represents a primitive toothed-whale group and a cetothere announces the presence of early whalebone whales.

MIOCENE

The Miocene is an epoch of considerable length and one represented by numerous and varied faunas in a number of regions. European localities are most abundant in France and Germany. St. Gérand, Sansan, and Simorre are among famous French localities of varied ages, and the various Molasse deposits and those of the Mainz basin and Steinheim are among the familiar fossiliferous beds of the German region. The Miocene is poorly represented in Africa, although there are scattered areas of this age in Egypt and in eastern and southwestern Africa. In Asia, too, the Miocene is present in but few places. The Loh and Tung Gur beds represent the last of the sequence of Mongolian deposits; the Bugti beds of Baluchistan have yielded a few mammals. In the late Miocene, however, we see the beginning of the deposits of the Siwalik Hills in India, which continue from this date to the Pleistocene.

In North America a major portion of the Miocene beds lies in the Great Plains area; they include such well-known deposits as the Harrison, Rosebud, Sheep Creek, Marsland, and Pawnee Creek. In Oregon the fossiliferous portion of the John Day beds are early Miocene. Florida in the Miocene has yielded the only good fauna found in eastern America in any stage of the Tertiary.

In South America the Miocene opened with a marine invasion represented by the Patagonian formation; following this were deposited the Santa Cruz of Patagonia, with a rich and varied fauna, and later beds of lesser importance.

The Miocene faunas are greatly "modernized" as compared with conditions at the beginning of the preceding epoch. During or at the end of the

Oligocene there had become extinct a score of families of more or less archaic types, particularly among the ungulates. Among the victims were the last amblypods, the pyrotheres, older proboscidean types; titanotheres, hyracodonts, and lophiodonts; primitive bunodont artiodactyls and primitive ruminants such as anoplotheres, xiphodonts, and amphimerycids; several primitive rodent families; the last of the archaic primate groups which characterized the Paleocene and Eocene. As a result of these extinctions and of new evolutionary developments we find that, in the known Miocene faunas as a whole, half of the living families of terrestrial mammals were then in existence and that these likewise constituted a good half of the faunal assemblage. If the peculiar South American types be excluded, the modern note is more marked; in the Northern Hemisphere only a quarter of the fauna is made up of families which have failed to survive.

We have noted the nearly complete isolation of the two hemispheres during the Oligocene; as a result, the Palaearctic and Nearctic faunas at the opening of the epoch differed widely in many respects. There are, however, indications of some intermigration during the early Miocene and again toward its close, which tended to reduce to some degree the faunal differences. The evidence suggests free communication between Africa and Eurasia during this epoch, but South America and Australia were still entirely separate evolutionary areas.

As before, the differences between North America and Eurasia were relatively small among the nonungulate orders, although even in cases where families were common to both areas the genera present were usually distinct. The creodont carnivores had disappeared except for lingering hyaenodonts in the Old World tropics. Varied dogs were present, including large "bear-dogs" and, in the late Miocene, such forms as *Hemicyon*, which appear close to the origin of the Ursidae. Mustelids, too, flourished, and felids, including true saber-tooths and pseudo saber-tooths, such as *Nimravus* of North America and *Pseudaelurus* in Europe. In the Old World the civets persisted, and from them had evolved, by the end of the Miocene, the first hyenas; in North America, in contrast, the early Miocene shows the beginning of the procyonids in *Phlaocyon* and other genera. Lagomorphs, rats, and primitive beaver-like forms (*Steneofiber*, *Palaeocastor*) are among common rodents.

Before the close of the Oligocene, primates had disappeared from North America. In the Eastern Hemisphere, however, the evidence, scanty though it is, tells of a considerable amount of evolution among the higher primates. *Pliopithecus*, a primitive gibbon, and *Dryopithecus*, an advanced manlike ape, appear in the European Miocene, and the discovery of several genera of these apes in the early Miocene of Africa suggests that this continent may have been an important center of primate evolution.

As in the Oligocene, there is a marked difference between the two northern continental areas in ungulate evolution, and there are marked differences between early and late faunas. Among the perissodactyls, rhinoceroses are present in both hemispheres. *Diceratherium* is the common American genus in the early Miocene; *Baluchitherium* persisted into the Miocene of Asia; more normal genera, *Aceratherium* and similar forms, are found in both areas but are more common in Eurasia. A last amynodont appears in the Miocene of Asia. *Macrotherium* and *Moropus* represent the chalicotheres in Eurasia and North America, respectively; tapirs are present in both areas.

Miocene horse history is mainly an American story. *Miohippus* persisted into the early Miocene and gave rise to *Anchitherium* and *Hypohippus* as larger forms of the same primitive type. *Parahippus*, first of horses with high-crowned teeth and reduced side toes, appeared at the beginning of the Miocene and still more advanced genera, *Merychippus* and *Pliohippus*, are characteristic of the American late Miocene. With the extinction of the palaeotheres, Eurasia had become barren of equoids, but *Anchitherium* successfully migrated to the Eastern Hemisphere and is present there in many Miocene localities.

The two areas have little in common as regards artiodactyls. Entelodonts made their last appearance in both areas, however, in the Lower Miocene; *Dinohyus* was a giant American form. The common bunodonts were swine in Eurasia, peccaries in North America; *Listriodon* and *Palaeochoerus* were representative piglike forms. Anthracotheres are absent in North America and in Europe, as well, beyond the Lower Miocene, but they survived in southern Asia and in Africa. In Europe, *Caenotherium* was present in the Lower Miocene as the last of nonpecoran selenodonts in that area; in America, in sharp contrast, there were abundant and varied camels, such as *Stenomylus* and *Oxydactylus*, and numerous oreodonts, including *Promerychochoerus*, *Merychyus*, etc. In both hemispheres primitive pecorans of the tragulid or hypertragulid groups survive but are uncommon.

In the Miocene are found the first stages in the deployment of higher ruminants. The earliest Miocene of both hemispheres witnesses the appearance of those types here included in the Palaeomerycidae: in Europe, *Dremotherium* and *Amphitragulus* and, somewhat later, *Palaeomeryx;* in America, *Blastomeryx*, followed by other deerlike forms. Later in the Miocene appear the first (and relatively rare) representatives of the living higher pecoran families. In Eurasia are primitive antelopes such as *Protragocerus*, primtive deer as *Dicrocerus*, and *Palaeotragus*, the first giraffid. These forms are absent from America; instead, we find *Merycodus* as the first of the prongbuck family.

A new element in the ungulate fauna of the northern continents is the advent of the proboscideans, previously known only from Africa. *Dinotherium*, with its peculiar lower tusks, bunodont mastodonts, such as *Gompho-*

therium and *Serridentinus*, and the lophodont *Mastodon* all appeared in Europe early in the Miocene and persisted throughout that epoch. In America their advent was retarded until the middle or end of the Miocene; *Dinotherium* failed to penetrate to America.

The Miocene Santa Cruz fauna is the best known of South American mammal assemblages. Marsupial carnivores and hystricoid rodents were numerous and varied. Edentates were abundant for the first time; forms, mostly of relatively small size, represent not only armadillos but anteaters, glyptodonts, and all three families of ground sloths. Litopterns were at the peak of their development, including, for example, *Diadiaphorus* and the pony-like *Thoatherium* among the proterotheres and *Theosodon* of the more heavily built macraucheniid family. Pyrotheres were extinct, but *Astrapotherium* was a giant end-form of another archaic line. Notoungulates were now much less varied in the number of families represented and were, in general, small in size; in number of individuals present, however, they bulk large in the faunal picture. *Homalodotherium*, the toxodonts *Adinotherium* and *Nesodon*, *Pachyrukhos*, and *Protypotherium* are representative genera.

In *Homunculus* we see the first representative of the platyrrhine monkeys of South America. The early history of this group is as puzzling as that of the hystricoid rodents. Perhaps the advent of the platyrrhines took place by invasion in some such fashion as that suggested for the rodents an epoch earlier. But primate remains are rare also in later South American sediments, and it is possible that ancestral primates were present earlier in the Tertiary in more wooded tropical areas.

Marine mammal-bearing deposits are present in many regions; the Calvert cliffs of Maryland, the Patagonian beds of South America, the Aquitanian basin of France, and the Antwerp basin of Belgium are among the prominent sources of fossil marine mammals. A lingering archaeocete was present in the early Miocene, but the epoch was one of rapid expansion of higher cetacean groups; the order was seemingly never more abundant or varied than at that time. Nearly every family of toothed and whalebone whales had appeared by the end of the Miocene. The squalodonts, primitive toothed whales, are common even in the earliest Miocene; and dolphins, ziphiids, and sperm whales are found in increasing numbers in later formations. The cetotheres, primitive whalebone whales, were abundant in the late Miocene, and there were even rare representatives of the living families of this suborder. *Halianassa* and other sirenians were present. The Miocene is further notable for the appearance of the first pinnipeds, including both eared and earless seals, and the first walrus, *Prorosmarus*.

PLIOCENE

The Pliocene is a relatively short epoch. Late beds, forming a transition to the Pleistocene, will be mentioned separately; the characteristic Pliocene fauna is that of the early part of the epoch, known in Eurasia as the Pontian age. Deposits containing this fauna are found widely distributed throughout the Mediterranean region and in eastern and central Europe; Eppelsheim, various localities in the Vienna basin, and Pikermi and Samos in the Aegean are among the best-known localities. To the eastward this same fauna extends through Persia (Maragha) and the Siwaliks to rich early Pliocene deposits in Honan and Shansi in China. Somewhat later European levels are best represented in southern France, as at Perpignan; in India the Siwalik series continues throughout the Pliocene; and there are scattered later Pliocene deposits in China. The Pliocene of Africa is almost unknown.

In North America there are numerous Pliocene deposits, the greater part of them in the Great Plains region. The earlier part of the epoch is represented in the Clarendon beds of Texas, the Snake Creek of Nebraska, and the Santa Fe beds of central New Mexico; a later stage in such formations as the Hemphill of the Texas Panhandle and the Republican River beds of Kansas.

In South America the long series of Patagonian sediments ceases at about the end of the Miocene, and the principal Pliocene areas are found farther to the north in Argentina. In the Andes foothills a set of beds often termed the Araucanian series covers nearly the whole length of the Pliocene; Monte Hermoso in the southern Pampas and the Entererrian region of northeastern Argentina also have characteristic deposits of this epoch.

The Pliocene fauna of the Northern Hemisphere is in great measure one of modern type. There had been a considerable elimination of old families, particularly of ungulates, during or at the close of the Miocene. The last amynodonts, entelodonts, caenotheres, and hypertragulids had been eliminated in the northern continental areas; the last archaic archaeocetes had disappeared from the oceans; and in South America astrapotheres, homalodotheres, notohippids, and interatheres are absent from the ungulate roster. The fauna is in the main one of modern families. Excluding South America and Australia, 80 per cent of the families of terrestrial mammals then present are types still extant; and, while a number of living families are not represented by Pliocene fossils, these are mainly rare and obscure groups. The Pliocene faunas further show much similarity generically to modern times; many familiar living genera, particularly among the carnivores and rodents, had arisen before the period was over, and in other cases generic differences between modern and Pliocene types are small.

There is evidence that a limited amount of faunal interchange took place between Eurasia and North America at the beginning of the Pliocene, but for most of the duration of the epoch there is little evidence of further connections. Old and New Worlds show many faunal similarities, but these can be attributed in the main to persistence of types interchanged during the late Miocene, and the genera present are usually distinct in the two regions.

The carnivores have run a parallel course in both continents. There are numerous canids and mustelids. Felids close to the living genera are present, in addition to saber-tooths. Primitive bears have appeared. Hyenas are prominently represented in Eurasia. There are a variety of bunodont mastodonts in both continents. *Hypohippus*, descended from *Anchitherium* of the Miocene, is present in Asia as in North America; and *Hipparion*, a lightly built, three-toed horse, reached Eurasia from North America and became widespread and common there. Rhinoceroses are present in both regions but are rare in North America; chalicotheres survive in both hemispheres, as do a few palaeomerycids. In Pontian times a nearly homogeneous fauna is found all the way from Spain to China and may well have been characteristic of Africa as well, for it is one quite similar in many respects to that found in Africa today. Elements in common with North America were noted above, but the presence of *Hipparion* as a characteristic Pontian form deserves emphasis. A striking feature is the abundance of bovids; several score of genera of antelopes have been described from the Pontian. Primitive genera of deer are common, as are the pigs and, in Asia, varied giraffids, including giant-horned forms. The peculiar proboscidean *Dinotherium* was still present, and in the eastern area primitive elephants, such as *Stegodon*, make their appearance.

In North America we find an ungulate assemblage still differing markedly from that of Europe. Not a bovid is present, or a true cervid. Instead, there is a great radiation of antilocaprids with varied types of horns, a last protoceratid, and a few final representatives of the oreodonts. Camels still flourished in a variety of forms, and peccaries were not uncommon. Horses of varied types were especially abundant, including hold-overs from the Miocene, as well as the *Hipparion* group and types progressing toward the modern one-toed forms.

There is evidence that the South American land bridge was now in process of re-establishment after the lapse of most of the Tertiary, for a first ground sloth had appeared in North America by mid-Pliocene times and a glyptodont at the end of the epoch.

In South America the Araucanian faunas of the early and middle Pliocene show evidence of this faunal interchange in the presence of a number of raccoon types, which may have used a Central American island chain as stepping stones. The fauna was otherwise purely native in character. A number of Miocene families of ungulates had disappeared, but other types of hoofed mammals still flourished, and the edentates and the hystricoid rodents were highly varied; in many instances there was a strong tendency toward large size. The borhyaenid marsupials still functioned as the carnivores of the faunas, and the evolution of a marsupial saber-tooth is an interesting development.

In the sea the archaeocetes were extinct, and the primitive squalodont whales were reduced and had vanished by the end of the Pliocene; ziphiids were fewer, and the various dolphin types were less numerous. Sperm whales, however, continued in fair numbers. Among the whalebone whales, a few final members of the cetotheres survived; they were being replaced by more abundant balaenids and balaenopterids.

In most continents beds are present which are transitional from Pliocene to Pleistocene; they are here included in the former epoch, but their position is much disputed. In Europe this is the Villafranchian stage, best known in the Arno Valley in Italy. Corresponding horizons are known in southern and eastern Asia; in America this terminal Pliocene is known in the Blanco beds of Texas and similar deposits in Kansas, Idaho, and Arizona. The fauna includes a mixture of characteristic Pliocene types with genera typical of Pleistocene and modern times. The period was apparently one of rising lands, with the re-establishment of the Bering Strait bridge. This is indicated by the fact that the modern horse genus, *Equus*, appears to have developed at this time in North America and had rapidly spread through the Old World to become a "type fossil" for this stage and the typical Pleistocene beds which follow.

In South America, too, the latest Pliocene, represented by the older beds of the Pampas—the Chapadmalal—is a time of transition. The earlier Pliocene "natives" are still present, except for the proterotheres. But in these deposits are also found numerous invaders from the north. Felids, normal and saber-toothed, and bears, as well as procyonids, are among the invading carnivores; horses, peccaries, and deer have entered to compete with native ungulates, and varied mice to rival the hystricoids. The end is in sight for much of the native population.

PLEISTOCENE

This shortest of Cenozoic epochs includes only the period of the Ice Age of northern regions and was, at the most, a million years or so in length. In the Pleistocene we reach a climax in the development of steep climatic gradients—a development which appears to have been in process of establishment during the later Tertiary. Arctic, temperate, and tropical zones were well differentiated. Their boundaries fluctuated considerably during the course of the Pleistocene. The evidence indicates that there were four successive southward advances of ice caps which covered much of Europe and North America. Contemporaneous with these advances were the development of great areas of tundra, local glaciations in more southerly mountain masses, and a shifting of climatic zones so that areas such as the Sahara and the deserts of the southwestern United States were, for the time, well watered. Between the periods of glaciation were three interglacial stages, during which zonal boundaries shifted far to the north, so that essentially tropical conditions were to be found over great parts of Europe and North America.

As a consequence of these climatic conditions, our treatment of faunal assemblages in the Pleistocene must be on a somewhat different basis from that used in the discussion of earlier Tertiary epochs. There we were able to consider the fauna of a continental area as essentially a unit; in the Pleistocene, however, divisions by climatic zones are prominent in the faunal picture. In both Eurasia and America the Arctic fauna was (and is) a very meager one; the temperate-zone fauna was much restricted in many ways, particularly as regards ungulates; various groups once widespread over much of the northern continental areas had retreated to the tropics, to reappear in the north, if at all, only during the warm interglacial stages.

Complete extinction of mammalian groups—families or higher categories—was relatively rare during or at the close of the Pliocene. Definite extinction may be noted in the case of the borhyaenid marsupials in South America, replaced by incoming fissipede placentals; of the last tropical survivor of the old creodonts; of the proterotheriid litopterns in South America; and, in North America, of two native ruminant families—the oreodonts and the protoceratids. There is, however, a very significant reduction in many groups—a reduction in numbers of genera or of areas of distribution. Rhinoceroses had made their last appearance in North America; *Dinotherium* had gone from Eurasia; in South America the macraucheniid litopterns were reduced in numbers; and still further reduction took place among the notoungulates. The variety of mastodonts had decreased before the opening of the Pleistocene. In the Old World, anthracotheres and chalicotheres were close to extinction; rhinoceroses, tragulids, and giraffids reduced. The typical Pliocene horses had become extinct, except for sparse records of *Hipparion* in the early Pleistocene or in transitional beds.

In any region where the fauna is adequately known, we find, in the Pleistocene, representatives of all the types now present. But, in addition, there are invariably numerous animals now extinct; and most of these are of large size.

The Pleistocene giants include representatives of almost every order of mammals: giant deer in both Eurasia and North America; the largest of proboscideans and of edentates. Large types were present among the South American rodents, and there were giant beavers in both Europe and North America. In Australia there were giant kangaroos and wombat-like forms and even an "outsized" *Ornithorhynchus*. Nor were the primates exempt. Madagascar lemurs included forms as large as the great apes, and there is recent evidence in southeastern Asia of giant human or subhuman types.

Apart from these large forms, since extinct, the Pleistocene assemblage—

particularly that of the later Pleistocene—was one with an air of familiarity about it. The time since the close of that epoch has been too short for any major evolutionary advance to have taken place, and hence it is not surprising that not merely most of the genera but also many of the species living today were common members of the Pleistocene faunas.

In the Pleistocene the northern continents were more united faunally than they had been since the earliest Tertiary. There had been considerable exchange between the two hemispheres in late Pliocene days, and the Bering Strait bridge appears to have been in existence during much of the Pleistocene, permitting further intermigration. Climatic conditions, however, were a strong limiting factor here. Arctic types and temperate-zone forms accustomed to cold climates and rugged terrain could cross this region readily; plains animals would find passage difficult; tropical forms were barred.

The Palaearctic and Nearctic regions had, in the Pleistocene as today, many groups in common and with generic identity in many cases. A few, such as the woolly mammoth and the musk oxen, found from England to New Mexico, were arctic types; others were groups familiar in temperate zones or climatically ubiquitous. Among essentially temperate-zone types of Eurasian origin we may note the deer and more northerly types of bovids, such as sheep, bison, and goats; the first reached North America in late Pliocene and Pleistocene times, and the bison became the commonest of American ungulates; and, while true goats did not make the passage, the related *Oreamnos*, the mountain "goat," did.

Groups already present in both areas and, in general, more tolerant of changing climatic surroundings are numerous. Such include varied sciuromorph and myomorph rodents; lagomorphs; canids; true cats, large and small; persistent saber-tooths; many mustelids. Pliocene mastodont types persisted into the early Pleistocene in both continents, and the true *Mastodon* was a late survivor in North America. Elephants, presumably of Asiatic origin, made the crossing to North America, and several types of mammoths, in addition to the woolly variety, were present in Old and New Worlds. Tapirs were present in both Eurasia and the Americas; true horses of the genus *Equus* flourished in both areas; camels, still present in their American homeland, made the passage to Eurasia.

Despite the many resemblances due to earlier as well as to Pleistocene interchanges, Old and New World faunas differed in a number of respects. Some of the contrasting types, such as the woolly rhinoceros and the giant tundra-dwelling *Elasmotherium* of Eurasia, were cold-climate forms. Most, however, were warmth-loving animals, many of them relatively recent in their development; even in the Pliocene, it would seem, the Siberian-Alaskan bridge was a difficult route for such animals to travel and in the Pleistocene was impossible.

With the coming of the Ice Age, many elements of the Pliocene Eurasian fauna were driven southward. A few of these forms, such as the hippopotami, hyenas, and southern genera of rhinoceroses ventured north again during the warm interglacial stages. Others never returned. They were, for the most part, confined to the southern regions of Asia and of Africa. Many of the types found in the Pleistocene in these areas have survived to modern times. Among these may be mentioned a varied series of primates, including great apes, cercopithecid monkeys, and lemurs; abundant antelopes; viverrids; pangolins; aardvarks. As has been said, this tropical fauna is markedly similar to the older Pontian fauna once widespread in more northerly regions. This similarity is enhanced by the persistence in the tropics during the Pleistocene of a number of archaic mammalian types which have since become extinct, such as *Dinotherium* and the last anthracotheres and chalicotheres.

In North America, as in Eurasia, peculiar indigenous mammalian types persisted in the Pleistocene. Such forms were, however, fewer in number than in the Old World; the more prominent forms are the peccaries, native geomyoid rodents, and antilocaprids, of which several genera were present. More notable was a considerable influx of South American mammals which had traveled northward over the Central American land bridge. A variety of ground sloths—*Megatherium*, *Mylodon*, *Megalonyx*, *Nothrotherium*—were common mammals; and glyptodonts and armadillos, large and small, were present in the Gulf region. Of hystricoid rodents only the porcupine entered northern areas. It is not improbable that the Pleistocene and Recent opossums of North America are reimmigrants from the south.

A great host of northern invaders entered South America in the Pleistocene and are abundant fossils in such superficial deposits as those of the Argentine and Uruguayan pampas and the Tarija beds of Bolivia. Of carnivores, the mustelids, the dogs, and the saber-tooth *Smilodon* had joined the procyonids, cats, and bears already present and presumably made havoc among the native animals. Competition of newcomers with the native herbivores was increased with the incoming of tapirs, peccaries, and llamas to join the horses and deer, which had entered in the late Pliocene. Mammoths failed to gain entry, but several mastodonts were present, and among the smaller mammals there were numerous invading mice and lagomorphs.

Of the old natives of South America, the hystricoid rodents, the monkeys, and the opossums appear to have been little affected. The edentates were seemingly in vigorous condition; for, in addition to the smaller types—armadillos, anteaters, tree sloths—the Pleistocene fauna included a variety of ground sloths and glyptodonts, unaware (so to speak) of their approaching extinction. On the other hand, the native ungulates were already close to the vanishing-point. Of the great array of families and orders present in the earlier epochs, there are but half-a-dozen genera still present—these including the litoptern *Macrauchenia* and the notoungulates *Toxodon* and *Typotherium*. Pleistocene and Subrecent cave deposits in the West Indies indicate that by some route a variety of small sloths and hystricoid rodents, nearly all now extinct, had reached those islands.

The Tertiary history of Australia is practically unknown; in the Pleistocene, when we first see the Australian mammal assemblage, it was in great measure that found today: monotremes; a great variety of marsupials, both carnivorous and herbivorous; of terrestrial placentals only a restricted series of rats and—presumably fellow-entrants in the late Pleistocene—man and dog. A feature of the Pleistocene here, as elsewhere, is the development of giant types, such as the marsupials *Diprotodon* and *Thylacoleo*.

Man appears to have been essentially a Pleistocene development. His homeland was surely some portion of the Eurasian-African land mass, and this area marks the limit of his spread for most of the Pleistocene. Australia, as far as we now know, was entered late in that epoch, and America not until the end of the Pleistocene, at the earliest.

RECENT

The Recent fauna of the world is marked, apart from the spread of mankind, by a relative paucity in its mammalian population. There are presumably no living types which were not also present in the Pleistocene, but many forms then present are now extinct. These were mainly mammals of large or more than average size. We may list the more conspicuous of the absent groups: the giant marsupials and monotremes of Australia; the sabertooths; the last of the South American ungulates; the ground sloths and glyptodonts; all the proboscideans except the two surviving elephants; the chalicotheres; the sivatheres; the anthracotheres; giant cervids; giant beavers. Regionally, too, there has been much extinction among groups formerly widespread. The range of the surviving proboscideans is a greatly restricted one; camels and tapirs disappeared from North America, peccaries from much of this region, horses from both Americas; rhinoceroses and hippopotami from much of Eurasia.

The reasons for this extinction of large mammals is difficult to discern. It was not altogether a matter of climatic vicissitude due to the Ice Age, for many of the extinct proboscideans survived to the end of the Pleistocene; and horses, camels, and ground sloths may have persisted in the American Southwest until very late times. Nor can we believe that disease can have been a major factor; for a disease which would attack such a variety of large animals and leave small ones untouched would be peculiar indeed. The spreading of mankind, *Homo sapiens*, is the only new feature seen in the late Pleistocene. Man may perhaps be responsible in some degree for this catastrophe; but his influence at the most must have been an indirect one.

CLASSIFICATION OF VERTEBRATES

Below is given a classification of vertebrates which includes a comprehensive (although by no means complete) list of genera known as fossils, together with a brief record of the ages and areas of their occurrences. It will be understood that such a compilation cannot well be completely critical or exhaustive and hence undoubtedly contains inaccuracies and omissions. To place the fossil forms in proper perspective, all families of vertebrates are listed (with their present distribution) whether they include fossil forms or not.

Abbreviations.—*Geological:* Carb., Carboniferous; Cret., Cretaceous; Dev., Devonian; Eoc., Eocene; Jur., Jurassic; L., Lower; M., Middle; Mioc., Miocene; Miss., Mississippian; Olig., Oligocene; Ord., Ordovician; Paleoc., Paleocene; Penn., Pennsylvanian; Perm., Permian; Pleist., Pleistocene; Plioc., Pliocene; R. Recent; Sil., Silurian; Tert., Tertiary; Trias., Triassic; U., Upper.

Geographical: Af., Africa; Ant., Antarctica; Arc., Arctic; As., Asia; Atl., Atlantic; Aus., Australia; CA., Central America; Cos., Cosmopolitan; EAs., East Asia; EInd., East Indies; Eu., Europe; Gr., Greenland; Ind., Indian; Mad., Madagascar; NA., North America; NAf., North Africa; NAs., Northern Asia; NAtl., North Atlantic; NPac., North Pacific; NZ., New Zealand; Oc., Ocean(s); Pac., Pacific; SA, South America; SAf., South Africa; SAs. Southern Asia; SAtl., South Atlantic; SPac., South Pacific; Spitz., Spitzbergen; WAs., Western Asia; WInd., West Indies; WNA., Western North America.

CLASS AGNATHA

SUBCLASS CEPHALASPIDOMORPHI

Order Osteostraci. F. **Tremataspidae**, *Tremataspis* U. Sil. Eu. F. **Dartmuthiidae**, *Dartmuthia Didymaspis Rotsikuellaspis* U. Sil. Eu. F. **Oeselaspidae**, *Oeselaspis* U. Sil. Eu. F. **Cephalaspidae**, *Aceraspis Ateleaspis Hemicyclaspis Micraspis Saaremaaspis Sclerodus* [*Eukeraspis*] *Thyestes* [*Auchenaspis*] *Witaaspis* U. Sil. Eu., *Hoelaspis* U. Sil. Spitz., *Cephalaspis* U. Sil.-L. Dev. Eu. Spitz., L. Dev. EAs., L.-U. Dev. NA, *Boreaspis Kieraspis* U. Sil.-L. Dev. Spitz., *Benneviaspis Securiaspis* U. Sil. Spitz., L. Dev. Eu.

Order Anaspida. F. **Birkeniidae**, *Saarolepis* [*Anaspis*] *Birkenia Pharyngolepis Pterolepis Rhyncholepis* U. Sil. Eu., *Ctenopleuron* U. Sil. NA. F. **Euphaneropsidae**, *Euphanerops* U. Dev. NA. F. **Lasaniidae**, *Lasanius* U. Sil. Eu. F. **Endeiolepidae**, *Endeiolepis* U. Dev. NA.

Order Cyclostomata

suborder myxinoidea. F. **Bdellostomatidae**, R. Oc. F. **Myxinidae**, R. Oc.

suborder petromyzontia. F. **Petromyzontidae**, R. Oc. Eu. NA. SA. Aus. NZ.

SUBCLASS PTERASPIDOMORPHI

Order Heterostraci. ?F. **Astraspidae**, *Astraspis* U. Ord. NA. F. **Poraspidae**, *Dinaspidella* [*Dinaspis*] *Homaspis* [*Homalaspis*] U. Sil. Spitz., *Anglaspis Ctenaspis*

Irregulareaspis [*Dictyaspis*] *Poraspis* [*Holaspis*] U. Sil. Spitz. Eu., *Americaspis* [*Palaeaspis*] U. Sil. NA. ?Eu., *Bryantaspis* [*Cryptaspis*] L. Dev. NA. **F. Cyathaspidae,** *Archegonaspis Corvaspis Cyathaspis Tolypelepis* [*Tolypaspis*] *Traquairaspis* U. Sil. Eu., *Diplaspis Eoarchegonaspis* U. Sil. NA., *?Orthaspis* L. Dev. Eu., *Cardipeltis* L. Dev. N.A., *Hibernaspis* L. Dev. NAs. **F. Pteraspidae,** *Brachipteraspis* U. Sil.–L. Dev. Eu., *Pteraspis* U. Sil.–L. Dev. Eu., L. Dev. NA., *Dyreaspis* L. Dev. Spitz., *Podolaspis Rhinopteraspis* L. Dev. Eu., *Protaspis* L. Dev. Eu. NA., *Eucyrtaspis* [*Cyrtaspis*] *Glossoidaspis* L. Dev. N.A., *Yolinia* M. Dev. Eu. **F. Drepanaspidae,** *?Eryptychius* U. Ord. NA., *Phialaspis Tesseraspis* U. Sil. Eu., *?Weigeltaspis* U. Sil.–L. Dev. Eu., *Drepanaspis Lophiaspis* L. Dev. Eu., *Psammosteus* M.–U. Dev. Eu., U. Dev. NA., Spitz., *Dyptychosteus Ganosteus* [*Pycnosteus*] *Placosteus Psammolepis Schizosteus* M. Dev. Eu., *Karelosteus* U. Dev. Eu. **F. Amphiaspidae,** *Amphiaspis* L. Dev. NAs.

ORDER COELOLEPIDA. **F. Thelodontidae,** *Coelolepis* U. Sil.–L. Dev. Eu., *Lanarkia Nostolepis Phlebolepis* U. Sil. Eu., *Thelodus* ?Ord. NA., U. Sil.–L. Dev. Eu. NA., ?U. Dev. Eu., *?Paraplesiobatis* L. Dev. Eu.

CLASS PLACODERMI

ORDER ACANTHODII. **F. Diplacanthidae,** *Dendracanthus Dontacanthus* U. Sil. Eu., *Climatius* U. Sil.–L. Dev. Eu., L. Dev. NA., *Onchus* U. Sil.–L. Dev. Eu., U. Sil.–U Dev. NA., *?Belacanthus Bradyacanthus ?Conolepis Euthacanthus Parexus ?Poracanthodes* L. Dev. Eu., *Nodacanthus* L.–U. Dev. Eu., M.–U. Dev. NA., *Homacanthus* L. Dev.–Miss. NA., M. Dev.–Penn. Eu., *Diplacanthus* [*Rhadinacanthus*] M. Dev. Eu., U. Dev. NA., *Devononchus* M.–U. Dev. Eu., *Haplacanthus* M.–U. Dev. Eu., M. Dev. Gr., *Marsdenius* Miss. Eu. **F. Ischnacanthidae,** *?Gomphodus* U. Sil.–L. Dev. Eu., *Ischnacanthus* ?U. Sil., L.–M. Dev. Eu. **F. Acanthodidae,** *Acanthoides* L. Dev. Eu., M. Dev. NA., *Cheiracanthus* L. Dev. NA., M.–U. Dev. Eu., U. Dev. Ant., Miss. Aus., Penn. NAs., *Mesacanthus* L.–M. Dev. Eu., U. Dev. NA., *Cheiracanthoides ?Helolepis* M. Dev. NA., *Acanthodes* [*Acanthoessus*] U. Dev.–Penn. NA., Miss.–L. Perm. NAs. Eu. Aus., L. Perm. Gr., *Eupleurogmus* Miss. Aus., *Holmesella* Penn. NA., *? Acanthodopsis Pseudacanthodes* [*Protacanthodes*] *Traquairichthys* [*Traquairia*] *Penn.* Eu. **F. Gyracanthidae,** *Gyracanthus* L. Dev.–Miss. NA., Miss.–Penn. Eu., *?Cosmacanthus* U. Dev. Eu., *Gyracanthoides* Miss. Aus. **?F. Onychodontidae,** *Onychodus* L. Dev. NAs. Spitz., L.–U. Dev. Eu., M.–U. Dev. NA. **?Acanthodii, incertae sedis:** *Ancistrodus Campylodus Stigmodus* U. Sil. Eu., *Plectrodus* U. Sil. Eu., M. Dev. NA., *Doliodus* L. Dev. NA., *Lophosteus* L. Dev. Eu., *Machaeracanthus* L.–M. Dev. Eu., L.–U. Dev. NA., *?Striacanthus* U. Dev. Aus.

ORDER ARTHRODIRA

SUBORDER EUARTHRODIRA

INFRAORDER ARCTOLEPIDA (ACANTHASPIDA). **F. Phlyctaenaspidae,** *?Palaeacanthaspis* U. Sil. Eu., *Anarthraspis Bryantaspis* [*Euryaspis*] L. Dev. NA., *Camptaspis* L. Dev. NA., *Euptychaspis* [*Ptychaspis*] L. Dev. NA., *Phlyctaenaspis* L. Dev. NA. Eu., ?M Dev. Aus., *Diadsomaspis Euleptaspis* [*Leptaspis*] *Kujdanowiaspis Prosphymaspis Taunaspis* L. Dev. Eu., *Arctolepis* [*"Acanthaspis" Jaekelaspis Heintzaspis*] *Lataspis* [*Plataspis*] *Svalbardaspis* L. Dev. Eu. Spitz., *Arctaspis Elegantaspis Heterogaspis* [*Monaspis*] *Huginaspis Mediaspis* L. Dev. Spitz., *Polyaspis* M. Dev. Spitz., *Actinolepis* M. Dev. Eu.

INFRAORDER BRACHYTHORACI. **F. Coccosteidae,** *Protitanichthys* M. Dev. NA., *Goniosteus Rhachiosteus Tropidosteus* M. Dev. Eu., *Coccosteus* M.–U. Dev. Eu. NA., Dev. Nova Zembla, *Dinichthys* [*Perissognathus*] M.–U. Dev. Eu. NAs., U. Dev. NA., *Copanognathus* [*Hussakofia*] *Gorgonichthys Heintzichthys* [*Stenognathus Machaerognathus*] *Holdenius Woodwardosteus* [*Liognathus*] U. Dev. NA., ?*Chelyophorus* U. Dev. Eu., *Pholidosteus* U. Dev. Eu. NA., *Groenlandaspis* U. Dev. Gr. **F. Titanichthyidae,** *Titanichthys* ?*Brontichthys* U. Dev. NA. **F. Mylostomidae,** *Dinognathus Dinomylostoma Mylostoma* U. Dev. NA. **F. Selenosteidae,** *Callognathus Gymnotrachelus Selenosteus Stenosteus* U. Dev. NA., **F. Pachyosteidae,** *Enseosteus Leiosteus Microsteus Pachyosteus Rhinosteus* U. Dev. Eu. **F. Hadrosteidae,** *Hadrosteus* U. Dev. Eu. **F. Leptosteidae,** *Leptosteus* U. Dev. Eu. NA. **F. Trematosteidae,** *Belosteus Brachyosteus Cyrtosteus Trematosteus* U. Dev. Eu. **F. Brachydiridae,** *Brachydirus* U. Dev. Eu. **F. Oxyosteidae,** *Oxyosteus* U. Dev. Eu. **F. Synaucheniidae,** *Synauchenia* [*Synosteus*] U. Dev. Eu. **F. Homostiidae,** *Homostius* M. Dev. Gr. Spitz., M.–U. Dev. Eu. **F. Heterostiidae,** *Heterostius* M. Dev. Gr. Spitz., M.–U. Dev. Eu. **F. Holonemidae,** *Angarichthys* L. Dev. NAs., ?*Aspidichthys* M.–U. Dev. NA., U. Dev. Eu., *Holonema* M. Dev. As., M.–U. Dev. Eu. NA., ?*Anomalichthys Megaloplax* U. Dev. Eu., *Deirosteus* U. Dev. Eu. NA., *Gyroplacosteus* U. Dev. Eu. Aus. **Incertae sedis:** *Diplognathus Glyptaspis Trachosteus* U. Dev. NA.

SUBORDER PTYCTODONTIDA. **F. Ptyctodontidae,** *Deinodus* M. Dev. NA., *Rhamphodopsis* M. Dev. Eu., *Rhynchodus* M.–U. Dev. Eu. NA., *Ptyctodus* M.–U. Dev. Eu. NA., U. Dev. NAs., *Eczematolepis* [*Palaeomylus Acantholepis Phlyctaenacanthus*] M.–U. Dev. NA., ?*Chelyophorus Rhamphodontus* [*Rhamphodus*] *Rhynchodontus* U. Dev. Eu., *Paraptyctodus* U. Dev. NA.

SUBORDER PHYLLOLEPIDA. **F. Phyllolepidae,** *Phyllolepis* [*Pentagonalepis*] U. Dev. Eu. NA. Aus. Gr.

ORDER MACROPETALICHTHYIDA (PETALICHTHYIDA). **F. Macropetalichthyidae,** *Lunaspis* L. Dev. Eu. NAs. Spitz., *Macropetalichthys* M. Dev. Eu. NA., *Notopetalichthys* M. Dev. Aus., *Epipetalichthys* M.–U. Dev. Eu.

ORDER ANTIARCHI. **F. Asterolepidae,** *Gerdalepis Microbrachius Pterichthyodes* [*Pterichthys*] M. Dev. Eu., *Asterolepis* M. Dev. Gr., U. Dev. Eu. *Bothriolepis* M.–U. Dev. NA. Eu., U. Dev. As. Aus. Ant. Af. Nova Zembla, *Cypholepis Taeniolepis* U. Dev. Eu. **F. Byssacanthidae,** *Belemnacanthus* [*Ceraspis Grossaspis*] M. Dev. Eu., *Byssacanthus* M.–U. Dev. Eu., *Lepadolepis* [*Ceratolepis*] U. Dev. Eu., *Byssacanthoides* U. Dev. Ant. **F. Remigolepidae,** *Remigolepis* U. Dev. Gr. Aus. ?NA.

ORDER STEGOSELACHII

SUBORDER STENSIOELLIDA. **F. Stensioellidae,** *Nessariostoma Pseudopetalichthys Stensioella* L. Dev. Eu. ?**F. Cratoselachiidae,** *Cratoselache* L. Carb. Eu.

SUBORDER RHENANIDA. **F. Gemuendinidae,** ?*Farnellia* U. Sil. Dev. Eu., ?*Conolepis Gemuendina* L. Dev. Eu., ?*Protodus* L. Dev. NA. Eu., *Asterosteus* M. Dev. NA. *Jagorina* U. Dev. Eu.

ORDER PALAEOSPONDYLOIDEA. **F. Palaeospondylidae,** *Palaeospondylus* M. Dev. Eu.

CLASS CHONDRICHTHYES

SUBCLASS ELASMOBRANCHII

ORDER CLADOSELACHII. **F. Cladoselachidae,** ?*Cladolepis*, ?*Ohiolepis* M. Dev. NA., "*Cladodus*" (pt.) M. Dev.–L. Perm. NA., U. Dev.–U. Perm. Eu., L. Perm. Gr., *Cladoselache* U. Dev. NA. Eu. ?*Tamiobatis* U. Dev. NA. **F. Ctenacanthidae,** "*Clado-*

dus" (pt.) M. Dev.–L. Perm. NA., U. Dev.–U. Perm. Eu., L. Perm. Gr., ?*Phoebodus* M. Dev.–Miss. NA., *Ctenacanthus* U. Dev. As., U. Dev.–L. Perm. NA., Miss.–Penn. Eu., *Goodrichia* Miss. Eu.

ORDER SELACHII.

SUBORDER HYBODONTOIDEA. **F. Coronodontidae,** *Coronodus* U. Dev. NA., ?*Denaea* Miss. Eu. **F. Tristychiidae,** *Tristychius* Miss. Eu. **F. Hybodontidae,** *Eoörodus* U. Dev. NA., *Protacrodus* U. Dev. Eu., *Desmiodus Hybocladodus Mesodmodus* Miss. NA., *Dicrenodus* [*Carchariopsis Pristicladodus*] Miss. NA. Eu., *Orodus* Miss. Eu., Miss.–Penn. NA., *Petrodus* Miss.–Penn. Eu., Penn. NA., *Symmorium* Penn. NA., *Hybodopsis Sphenacanthus* Penn. Eu., *Arctacanthus* [*Dolophonodus*] L. Perm. NA. Gr., *Wodnika* U. Perm. Eu., *Acrodus* ?Perm. As., L. Trias.–U. Cret. Eu., M. Trias.–U. Cret. NA., U. Trias. Spitz., U. Cret. SA., *Hybodus* L. Trias. Spitz. Gr., M. Trias.–U. Jur. NA., M. Trias.–U. Cret. Eu., U. Trias.–Jur. EAs., Jur.–Cret. Aus., U. Cret. NAf., *Polyacrodus* L. Trias. Gr., M.–U. Trias. Eu., *Lissodus* L. Trias. SAf., *Doratodus* M.–U. Trias. Eu., *Nemacanthus* M. Trias.–U. Jur. Eu., U. Trias. Spitz. NA., *Palaeobates* M. Trias. Eu. Spitz., *Carinacanthus* U. Trias. NA., *Asteracanthus* [*Strophodus*] U. Trias. NA., L. Jur.–L. Cret. Eu., Jur. EAs. Mad., U. Cret. NAf. *Bdellodus* L. Jur. Eu., *Orthacodus* U. Jur.–L. Cret. Eu., *Synechodus* L. Cret.–Eoc. Eu., U. Cret.–Eoc. NA. SA., U. Cret. NAf., Eoc. NZ. As., *Platyacrodus Pseudacrodus* U. Cret. SA. **F. Edestidae,** *Scoliorhiza* Miss. NA., *Edestus* Miss.–Penn. Eu., Penn.–L. Perm. NA., *Campodus* Miss.–L. Perm. Eu., Penn.–L. Perm. NA., *Lissoprion Toxoprion* Penn. NA., *Agassizodus* Penn. NA., L. Perm. Gr., *Helicampodus* Perm. SAs., *Helicoprion* L. Perm. Eu. As. EInd. Aus., *Parahelicoprion* L. Perm. Eu., *Fadenia* L. Perm. Gr.

SUBORDER HETERODONTOIDEA. **F. Heterodontidae (Cestraciontidae),** R. Oc., *Palaeospinax* L. Jur. Eu., *Heterodontus* [*Cestracion*] U. Jur.–Olig. Eu., U. Cret.–Eoc. Af., Mioc. SA. NZ. Aus., R. Pac. Oc. Ind. Oc., *Parapalaeobates* U. Cret. NAf.

SUBORDER NOTIDANOIDEA. **F. Hexanchidae (Notidanidae),** R. Oc., *Hexanchus* [*Notidanus*] M. Jur.–Plioc. Eu., U. Cret. WAs. NZ. Mad., U. Cret.–Olig. SA., Eoc. Af., Mioc. NA., R. Oc. **F. Chlamydoselachidae,** R. Oc., *Chlamydoselache* Mioc. WInd., Plioc. Eu., R. NAtl. NPac.

SUBORDER GALEOIDEA. **F. Carchariidae,** R. Oc., *Carcharias* [*Odontaspis*] L. Cret.–Plioc. Eu., U. Cret.–Mioc. SA., U. Cret.–Plioc. NA. NZ., U. Cret. As., Paleoc.–Plioc. Af., Mioc. Aus. WInd. **F. Scapanorhynchidae,** R. Oc., *Scapanorhynchus* [*Mitsukurina*] L.–U. Cret. Eu., U. Cret. As. Af. NZ. SA., Cret. ?Mioc. NA., U. Cret. Paleoc. WInd., R. Atl. NPac. **F. Isuridae (Lamnidae),** R. Oc., *Orthacodus* L. Jur.–U. Cret. Eu., U. Cret. NA., *Isurus* [*Otodus Oxyrhina Lamna*] L. Cret.–Plioc. Eu., U. Cret.–Mioc. Aus. As. SA., U. Cret.–Plioc. Af., U. Cret., Mioc. WInd., U. Cret.–Pleist. NA., Mioc. Mad., Mioc.–Plioc. NZ., R. Oc., *Carcharodon* U. Cret.–Pleist. Eu., Eoc.–Plioc. Af., Eoc.–Pleist. NA., Mioc. SA. EInd., Mioc.–Plioc. WInd. NZ., Plioc. EAs., R. Oc., *Squalicorax* [*Corax*] U. Cret. NAf. Mad. As. SA. WInd., U. Cret.–Eoc. NA., U. Cret.–Mioc. Eu., *Pseudocorax* U. Cret. Eu., *Hypotodus* Eoc.–Olig. Eu., *Carchariolamna* Mioc. SAs., *Carcharoides* Mioc. SA. Aus. **F. Cetorhinidae (Halsydridae),** R. Oc., *Cetorhinus* [*Halsydrus*] Olig.–Plioc. Eu., R. Oc. **F. Alopiidae,** R. Oc., *Alopias* [*Vulpecula*] Eoc. Af., Olig.–Mioc. Eu., R. Oc. **F. Orectolobidae,** R. Oc., *Crossorhinops* U. Jur. Eu., *Orectolobus* [*Crossorhinus*] ?U. Jur. Eu., R. Oc., *Ginglymostoma* U. Cret. WInd., U. Cret.–Eoc. Eu., Eoc. Af. NA., R. Oc., *Chiloscyllium* Mioc. Eu., R. Oc. **F. Rhincodontidae,** R. Oc. **F. Scylliorhinidae (Scylliidae),** R. Oc., *Palaeoscyllium* U. Jur. Eu., *Galeus* [*Pristiurus*] U. Jur.–Plioc. Eu., Eoc. NA. Af., R. Oc., *Cantioscyllium* U. Cret. Eu., *Mesiteia* U. Cret. WAs., Eoc. Eu., *Scylliorhinus* [*Scyllium Thyellina*] U. Cret. WAs. NA., U. Cret.–Plioc. Eu., Eoc. NAf., R. Oc. F. **Pseudotriakidae,** R. Oc. F. **Triakidae,** R. Oc., *Mustelus* Olig.–Plioc. Eu., R. Oc. F. **Galeolamnidae** (**Carcharinidae**), R. Oc., *Bidentulus* [*Bidentia*] Jur. Eu., *Galeocerdo* U. Cret.–Mioc. NA., Eoc.–Mioc. Af., Eoc.–Plioc. Eu., Mioc. As. SA. WInd., R. Oc., *Hemipristis* U. Cret.–Mioc. NA., U. Cret.–Plioc. Eu., Eoc.–Mioc. Af., Mioc. As. SA., Tert. EInd., R. Oc., *Pseudogaleus* Eoc. Eu., *Alopiopsis* Eoc. NAf., Eoc.–Olig. Eu., *Galeolamna* [*Aprionodon Carcharinus Eugaleus Hypoprion Prionodon*] Eoc. Af., Eoc.–Plioc. Eu. NA., Olig.–Mioc. SA., Mioc. WInd., R. Oc., *Hennigia* Mioc. Eu. F. **Sphyrnidae,** R. Oc. *Protosphyrna* U. Cret. SA., *Sphyrna* [*Zygaena*] U. Cret.–Mioc. NA., Mioc. Af., Mioc.–Plioc. Eu., R. Oc.

SUBORDER SQUALOIDEA. F. **Protospinacidae,** *Protospinax* U. Jur. Eu. F. **Squalidae** (**Spinacidae**), R. Oc., *Centrophorus* U. Cret. WAs., ?U. Cret., Mioc. Eu., R. Oc., *Spinax* [*Etmopterus*] ?U. Cret., Mioc. Eu., R. Oc., *Squalus* [*Acanthias*] U. Cret. WAs., U. Cret.–Plioc. Eu., Eoc. NAf., Olig. SA., Mioc. NA., R. Oc., *Oxynotus* [*Centrina*] Mioc.–Plioc. Eu., R. Oc. F. **Scymnorhinidae** (**Dalatiidae**), R. Oc., *Isistius* U. Cret.–Eoc. Af., Eoc. Mioc. Eu., R. Oc., *Scymnorhinus* [*Dalatius Scymnus*] U. Cret. WAs. NA., Eoc. NAf., Eoc.–Plioc. Eu., Mioc. NZ., R. Oc. F. **Echinorhinidae,** R. Oc., *Echinorhinus* Mioc. NA., Plioc. Eu., R. Oc. F. **Pristiophoridae,** R. Oc., *Marckgrafia* U. Cret. NAf., *Propristiophorus* U. Cret. WAs., *Pristiophorus* Mioc. Eu., R. Oc., *Pliotrema* Tert. NZ., R. Oc. F. **Rhinidae** (**Squatinidae**), R. Oc., *Rhina* [*Squatina*] U. Jur.–Plioc. Eu., U. Cret. WAs., U. Cret.–Mioc. NA., Eoc. Af., R. Oc.

ORDER BATOIDEA (HYPOTREMATA, RAJIFORMES). F. **Rhinobatidae,** R. Oc., *Asterodermus Belemnobatis Cyclarthrus* U. Jur. Eu., *Rhinobatis* [*Euryarthra Spathiobatis*] U. Jur.–Mioc. Eu., U. Cret. WAs., R. Oc., *Rhynchobatus Trygonorhina* Eoc.- Mioc. Eu., R. Oc. F. **Pristidae,** R. Oc., *Ischyrhiza* U. Cret. NA. SA., *Sclerorhynchus* U. Cret. WAs., *Schizorhina* U. Cret. Af., *Onchosaurus* [*Gigantichthys*] U. Cret. Eu. NAf., *Dalpiazia Ganopristis Onychopristis Peyeria* U. Cret. NAf., *Pristis* ?U. Cret., Eoc. NA., Eoc. Af., Eoc.–Mioc. Eu., R. Oc., *Anoxypristis* [*Oxypristis*] *Centropristis* Eoc. Eu., *Propristis* [*Amblypristis Eopristis*] Eoc. Af. F. **Discobatidae,** R. Oc., ?*Platyrhina* Eoc. Eu., R. Oc. F. **Rajidae,** R. Oc., *Raja* [*Actinobatis*] U. Cret. WAs. WInd., Paleoc.–Plioc. Eu., Eoc.–Mioc. NA., R. Oc., *Platyspondylus* U. Cret. NAf., ?*Platyrhina* Eoc. Eu., R. Oc., *Oncobatis* Plioc. NA. F. **Trygonidae** (**Dasyatidae**), R. Oc., *Trygon* [*Alexandrinum*] ?U. Cret. NAf., ?L. Cret., Eoc.–Mioc. Eu., Eoc.–Pleist. NA., R. Oc., *Parapalacobates* U. Cret. NAf., *Rhombodus* U. Cret. NAf. Eu. SA., *Ptychotrygon* U. Cret. Eu., *Myledaphus* U. Cret. NA., *Cyclobatis* U. Cret. WAs., *Hypolophites* ?U. Cret., Eoc. Af., *Xiphotrygon* [*Heliobatis*] Eoc. NA., *Taeniura* Eoc.–Plioc. Eu., R. Oc., *Urolophus* Eoc. Eu., Pleist. NA., R. Oc., *Hypolophus* Eoc. Eu., R. Oc., *Pteroplatea* Mioc. NA., R. Oc., *Gryphodobatis* Plioc. NA. F. **Potamotrygonidae,** R. SA., F. **Ptychodontidae,** *Hylaeobatis* L. Cret. Eu., *Heteroptychodus* U. Cret. EAs., *Ptychodus* U. Cret. Eu. As. NAf. EInd. NA., *Aulodus Hemiptychodus* U. Cret. Eu. F. **Myliobatidae,** R. Oc., *Myliobatis* L. Cret.–Plioc. Eu., U. Cret.–Mioc. NA., Eoc. Af., Mioc. As., Tert. NZ., R. Oc., *Apocopodon* U. Cret. SA., *Rhinoptera* [*Zygobates*] U. Cret. SA., U. Cret.–Eoc. Af., U. Cret.–Plioc. Eu., Eoc.–Mioc. NA., *Aetobatis* Paleoc.–Plioc. Eu., Eoc. Af., Eoc.–Pleist. NA., Mioc. As. SA., R. Oc., *Promyliobatis* Eoc. Eu., *Mesobatis* Plioc. NA. F. **Molbulidae,** R. Oc., *Manta* Plioc. NA., R. Oc. F. **Torpedin-**

idae, R. Oc., *Eotorpedo* Eoc. Af., *Torpedo* ?Eoc. Eu., R. Oc., *Narcine* Eoc. Eu., R. Oc., *Narcopterus* Eoc. Eu.

ORDER PLEURACANTHODII. **F. Pleuracanthidae,** *Pleuracanthus* [*Diplodus Dittodus Orthacanthus Xenacanthus*] U. Dev.–L. Perm. NA., Miss.–L. Perm., ?U. Trias. Eu., U. Trias. Aus.

SUBCLASS HOLOCEPHALI

ORDER BRADYODONTI. **F. Cochliodontidae,** *Helodus* [*Diclitodus*] U. Dev.–L. Perm. NA., Miss.–Penn. Eu., Perm. Aus., *Sandalodus* U. Dev.– Penn. NA., Miss. Eu., *Chitonodus Cochliodus Deltoptychius Oracanthus* Miss. Eu. NA., *Cladacanthus Eutomodus* [*Tomodus*] Miss. Eu., *Deltodopsis Periplectrodus* Miss. NA., *Deltodus Poecilodus Xystrodus* Miss. Eu., Miss.–Penn. NA., *Streblodus* Miss. Eu., Penn. NA., *Orthopleurodus Peripristis Vaticinodus* Miss.–Penn. NA., *Pleuroplax* Miss.–Penn. Eu., *Psephodus* Miss.–Penn. Eu. SAs., Miss.–L. Perm. NA., *Menaspis ?Rhadamas* U. Perm. Eu. **F. Petalodontidae,** *Euglossodus* [*Glossodus*] *Mesolophodus Pristodus* Miss. Eu., *Antliodus* [*Tanaodus*] *Petalorhynchus Polyrhizodus* Miss. Eu. NA., *Fissodus* Miss. Eu., Miss.–Penn. NA., *Climaxodus* Miss.–Penn. Eu., *Ctenopetalodus* Miss.–Penn. Eu. NA., *Callopristodus* Miss.–Penn. Eu., Penn. NA., *Petalodus* Miss.–Penn. NA., Miss.–L. Perm. Eu., *Ctenoptychius* Miss.–Penn. NA., Penn. Eu., U. Perm. Eu., *Janassa* Penn.–L. Perm. NA., Penn.–U. Perm. Eu., L. Perm. Gr., *Brachyrhizodus Megactenopetalus* L. Perm. NA. **F. Psammodontidae,** *Mazodus* Miss. NA., *Archaeobatis* ?Miss. NA., *Psammodus* Miss. NA. Eu., *Lagarodus* Miss.–Penn. Eu. **F. Copodontidae,** *Acmoniodus* U. Dev. NA., *Labodus* Miss. NA. Eu., *Copodus* Miss. Eu. NA., ?L. Perm. Gr., *Solenodus* Penn. Eu. **F. Chondrenchelydidae,** *Chondrenchelys ?Eucentrurus* Miss. Eu.

ORDER CHIMAERAE. **F. Squalorajidae,** *Squaloraja* L. Jur. Eu. **F. Myriacanthidae,** *Acanthorhina* L. Jur. Eu., *Myriacanthus* L.–M. Jur. Eu., *Chimaeropsis* L.–U. Jur. Eu. **F. Chimaeridae,** R. Oc., *Brachymylus* L.–U. Jur. Eu., *Pachymylus* M. Jur. Eu., *Ischyodus* M. Jur.–U. Cret. Eu., Cret. NZ., *Ganodus* U. Jur. Eu., *Elasmodectes* U. Jur.–U. Cret. Eu., *Edaphodon* L. Cret.–Mioc. Eu., U. Cret.–Eoc. NA., *Ichthypriapus Isotaenia Leptomylus Myledaphus* U. Cret. NA., *Chimaera* U. Cret. Aus., Eoc.–Plioc. Eu., Tert. NZ. EInd., R. Oc., *Callorhynchus* U. Cret. NZ., Mioc. SA., R. Oc., *Elasmodus* U. Cret.–Eoc. Eu., *Amylodon* Olig. Eu.

CHONDRICHTHYES OR PLACODERMI INCERTAE SEDIS—ICHTHYODORULITES

Bulbocanthus Helenacanthus Pinnacanthus L. Dev. NA., *Cyrtacanthus* M. Dev. NA., *Gamphacanthus* M.–U. Dev. NA., *Apateacanthus Hoplonchus Oestophorus* U. Dev. NA., *Heteracanthus* U. Dev. Eu. NA., *Stethacanthus* U. Dev.–Miss. NA., *Bythiacanthus Gampsacanthus Glymmatacanthus Lecracanthus Xystracanthus* Miss. NA., *Erismacanthus Geisacanthus* [*Cosmacanthus*] *Harpacanthus* Miss. NA. Eu., *Cynopodius Dipriacanthus Euphyacanthus Gnathacanthus Lispacanthus Margaritacanthus* [*Euacanthus*] *Stichacanthus* Miss. Eu., *Acondylacanthus Asteroptychius* Miss. Eu., Miss.–Penn. NA., *Physonemus* Miss. Eu., Miss.–Penn. NA., Penn. SAs., *Batacanthus* Miss.–Penn. NA., *Euctenodopsis Lepracanthus* Penn. Eu., *Euctenius Listracanthus* Penn. Eu. NA., *Macrodontacanthus Hamatus* L. Perm. NA., *Ancistriodus* L. Perm. NA. EInd., *Thaumatacanthus* Perm. SAs.

CLASS OSTEICHTHYES

SUBCLASS ACTINOPTERYGII

Superorder Chondrostei

Order Palaeoniscoidea. **F. Cheirolepidae,** *Cheirolepis* M. Dev. Eu., U. Dev. NA. **F. Rhadinichthyidae,** *Stegotrachelus* M. Dev. Eu., ?U. Dev. NA. Ant., *Rhadinichthys* U. Dev. NAs., U. Dev.–Penn. NA. Eu., Penn. SA., *Aetheretmon Cycloptychius Fouldenia Rhadinoniscus Strepheoschema* Miss. Eu., ?*Eurylepidoides* L. Perm. NA. **F. Canobiidae,** *Canobius Mesopoma* Miss. Eu. **F. Haplolepidae,** *Haplolepis Pyritocephalus* Penn. Eu. NA., *Phanerorhynchus* Penn. Eu. **F. Elonichthyidae,** *Elonichthys* ?U. Dev., Miss.–U. Perm. Eu., Miss.–Penn. NA., Perm. SA. SAf., L. Perm. Gr. U. Perm. Aus., *Drydenius* Miss. Eu., *Gonatodus* Miss. NA., Miss.–Penn. Eu., ?*Rhabdolepis* L. Perm. Eu., *Ganolepis* ?Perm. NAs. **F. Palaeoniscidae,** *Progyrolepis* Penn. Eu., *Palaeoniscus* U. Perm., ?L. Trias. Eu., *Glaucolepis* [*Pteronisculus*] L. Trias. Mad. Gr. Spitz., ? *Agecephalichthys* M. Trias. Aus., *Gyrolepis* M.–U. Trias. Eu., *Cosmolepis* [*Oxygnathus*] L. Jur. Eu. **F. Pygopteridae,** *Cosmoptychius Nematoptychius* Miss. Eu., *Pygopterus* U. Perm. Eu. Gr., L. Trias. Eu. Af. Spitz. **F. Acrolepidae,** *Watsonichthys* Miss. Eu., *Reticulolepis* Miss.–U. Perm. Eu., *Acrolepis* Miss.–U. Perm. Eu., L. Perm. NA. NAs. U. Perm. EAf., *Acropholis Plegmolepis* L. Perm. Gr., *Acrorhabdus* L. Trias. Spitz. Gr., ?*Hyllingea* U. Trias. Eu. **F. Amblypteridae,** ?*Commentrya* [*Cosmopoma Dipteropoma Elaveria*] ?*Paramblypterus* U. Penn. Eu., *Amblypterus* L.–U. Perm. Eu., ?L. Perm. NA. ?As., *Amblypterina* U. Perm. Eu. **F. Aeduellidae,** *Aeduella* ?*Westollia* [*Lepidopterus*] L. Perm. Eu. **F. Cryphiolepidae,** *Cryphiolepis* Miss. Eu. **F. Scanilepidae,** *Scanilepis* U. Trias Eu. Spitz. **F. Coccolepidae,** *Coccolepis* L. Jur.–L. Cret. Eu., M. Jur. NAs., Jur. Aus., *Palaeoniscionotus* Jur. NAs. **F. Dicellopygidae,** ?*Brachydegma* L. Perm. NA., *Dicellopyge* L. Trias SAf., ? *Aneurolepis* [*Urolepis*] M.–U. Trias. Eu. **F. Birgeriidae,** *Birgeria* [*Xenestes*] L.–U. Trias. Eu., L. Trias. Spitz. Gr. NA. **F. Holuridae,** *Holurus* Miss. Eu. **F. Tarrasiidae,** *Tarrasius* Miss. Eu., ?*Palaeophichthys* Penn. NA. **F. Boreolepidae,** *Boreolepis* U. Perm. Gr. **F. Trissolepidae,** *Trissolepis* [*Sphaerolepis*] Penn. Eu. **F. Tegeolepidae,** *Tegeolepis* [*Actinophorus*] Miss. NA. **F. Cocconiscidae,** *Cocconiscus* [*Coccocephalus*] Penn. Eu. **F. Cornuboniscidae,** *Cornuboniscus* Penn. Eu. **F. Styracopteridae,** *Benedenichthys* [*Benedenius*] *Styracopterus* [*Fouldenia*] Miss. Eu. **F. Amphicentridae,** *Cheirodopsis Proteurynotus* Miss. Eu., *Amphicentrum* [*Cheirodus*] *Plectrolepis* [*Eurynotus*] Miss.–Penn. Eu. NA., *Paraeurynotus* L. Perm. NAs., *Eurynotoides* U. Perm. Eu., *Glodulodus* [*Eurysomus*] U. Perm. Eu. **F. Platysomidae,** *Mesolepis Paramesolepis Wardichthys* Miss. Eu., *Platysomus* Miss.–U. Perm. Eu., ?L. Trias. Spitz. NA. **F. Dorypteridae,** *Dorypterus* U. Perm. Eu. **F. Carbovelidae,** *Carboveles* Miss. Eu., *Gymnoniscus* [*Phanerosteon*] Penn. Eu.

Order Polypterini. **F. Polypteridae,** R. Af., *Polypterus* Eoc.–R. Af.

Order Acipenseroidei. **F. Chondrosteidae,** ?*Psilichthys* Trias. Aus., *Chondrosteus Gyrosteus* L. Jur. Eu., *Stichopterus* Jur. As. **F. Acipenseridae,** R. Eu. As. NA., *Acipenser* ?U. Cret., Eoc.–R. NA., Eoc.–R. Eu., R. As. **F. Polyodontidae,** R. NA. EAs., *Pholidurus* U. Cret. Eu., *Crossopholis* Eoc. NA.

Order Subholostei. **F. Dictyopygidae (Catopteridae),** *Atopocephala Daedalichthys Helichthys* L. Trias. SAf., ?*Ischnolepis* ?L. Trias. Af., *Brookvalia* L.–M. Trias. Aus., *Beaconia Dictyopleurichthys Geitonichthys Molybdichthys Phlyctaenichthys Schizurichthys* M. Trias. Aus., *Dictyopyge* U. Trias Eu. NA. ?Aus., *Redfieldia*

[*Catopterus*] U. Trias. NA. **F. Perleididae,** *Chrotichthys Tripelta Zeuchthiscus* L. Trias Aus., *Pristisomus* L. Trias. Aus. Mad., *Meidiichthys* L. Trias. SAf., *Perleidus* L. Trias. Spitz. Gr. Mad., M.–U. Trias. Eu., *Dollopterus* ?L. Trias. NA., M. Trias. Eu., *Asterodon Crenilepis Nephrotus* M. Trias. Eu., *Manlietta Procheirichthys* M. Trias. Aus., *Colobodus Meridensia* M.–U. Trias. Eu., ?*Gigantopterus* U. Trias. Eu., ?*Thoracopterus* U. Trias. Eu., ?M. Trias. Aus. **F. Platysiagidae,** *Platysiagum* M. Trias.–L. Jur. Eu. **F. Cephaloxemidae,** *Cephaloxemus* M.–U. Trias. Eu. **F. Peltopleuridae,** ?*Habroichthys Peltopleurus Placopleurus* U. Trias. Eu. **F. Luganoiidae** *Luganoia* M.–U. Trias. Eu., *Besania* U. Trias. Eu. **F. Aetheodontidae,** *Aetheodontus* M.–U. Trias. Eu. **F. Ptycholepidae,** *Boreosomus* [*Diaphorognathus*] L. Trias. Mad. Gr. ?Spitz., ?*Leptogenichthys* M. Trias. Aus., *Ptycholepis* U. Trias.–L. Jur. Eu., U. Trias. NA. **F. Parasemionotidae,** *Parasemionotus Watsonulus* L. Trias. Mad. Gr., *Tungusichthys* L. Trias. NAs., *Broughia Helmolepis Ospia* L. Trias. Gr., *Promecosomina* M.–U. Trias. Aus. **F. Pholidopleuridae,** *Australosomus* L. Trias. Mad. Gr. SAf., *Macroaethes* M. Trias. Aus., *Pholidopleurus* M.–U. Trias. Eu., *Arctosomus* Trias. NAs. **F. Saurichthyidae,** *Saurichthys* [*Belonorhynchus*] L. Trias. Spitz. Gr. Mad., L.–M. Trias. Aus., L. Trias.–L. Jur. Eu., Trias. NA., *Acidorhynchus Gymnosaurichthys* L. Jur. Eu. **F. Cleithrolepidae,** *Cleithrolepis* L. Trias. SAf., L.–U. Trias. Aus., U. Trias. Eu., *Hydropessum* L. Trias. SAf., ?*Dipteronotus* U. Trias. Eu. **F. Bobasatraniidae,** *Bobasatrania* L. Trias. Gr. Mad. Spitz., *Ecrinesomus* L. Trias. Mad.

PALAEONISCOIDEA OR SUBHOLOSTEI INCERTAE SEDIS. *Aldingeria* Penn. Gr., *Apateolepis* M. Trias. Aus., *Atherstonia* U. Perm. Eu., L. Trias. SAf. Mad., *Belichthys* M. Trias. Aus., *Broometta* Trias. SAf., *Caruichthys* L. Trias. SAf., *Centrolepis* L. Jur. Eu., *Disichthys* Perm. SAf., *Elpisopholis* U. Trias. Aus., *Evenkia* L. Trias. NAs., *Geomichthys* Penn. Eu., *Gyrolepidotus* ?Perm. NAs., *Megapteriscus Mesembroniscus* M. Trias. Aus., *Myriolepis* L.–U. Trias. Aus., ?Penn. Eu., *Namaichthys* L. Perm. SAf., *Pelichthys* Perm. SAf., *Trachelacanthus* L. Perm. Eu.

SUPERORDER HOLOSTEI

ORDER SEMIONOTOIDEA. **F. Semionotidae,** *Acentrophorus* U. Perm. Eu., *Semionotus* [*Ischypterus*] L.–U. Trias. Eu., U. Trias. SAf. NA., *Eosemionotus* M. Trias. Eu., ?*Enigmatichthys* M. Trias. Aus., *Paralepidotus Serrolepis* M.–U. Trias. Eu., ? *Archaeosemionotus Sargodon Woodthorpea* U. Trias. Eu., *Dapedius* U. Trias.–L. Jur. Eu., L. Jur. As., *Lepidotus* [*Lepidotes*] U. Trias. SAf., U. Trias.–L. Cret., ?U. Cret. Eu., U. Trias.–L. Cret. NA., L. Jur. Mad., Jur. EAs., L. Cret. SA., *Sinosemionotus* M. Trias. EAs., *Tetragonolepis* L. Jur. Eu. As., *Heterostrophus* U. Jur. Eu. **F. Lepidosteidae,** *Lepidosteus* [*Lepisoseus Clastes*] U. Cret.–Mioc. Eu., U. Cret.–R. NA. Eoc. As.

ORDER PYCNODONTOIDEA. **F. Pycnodontidae,** *Eomesodon* U. Trias.–L. Jur. Eu., *Gyrodus* M. Jur.–L. Cret. Eu., U. Jur. ?U. Cret. NA., *Macromesodon* [*Mesodon*] M. Jur.–L. Cret. Eu., L. Cret. NA., *Athrodon* U. Jur.–L. Cret. Eu., *Mesturus* U. Jur. Eu., *Microdon* U. Jur.–L. Cret. Eu., L. Cret. NA., *Stemmatodus* ?U. Jur. L. Cret. Eu., *Coelodus* U. Jur.–U. Cret. Eu., L.–U. Cret. NA., U. Cret. WAs. NAf. Mad., *Anomoedus* L.–U. Cret. Eu. NA., U. Cret. NAf., *Pycnodus* L.–U. Cret. NA., L. Cret.–Eoc. Eu., Eoc. Af. As., *Coccodus Trewavasia* [*Xenopholis*] U. Cret. WAs., *Acrotemnus Polygyrodus* U. Cret. Eu., *Pycnomicrodon* U. Cret. NA., *Palaeobalistum* U. Cret. As. SA., U. Cret.–Eoc. Eu.

ORDER ASPIDORHYNCHOIDEA. **F. Aspidorhynchidae,** *Aspidorhynchus* U. Jur. Eu., *Belonostomus* U. Jur.–U. Cret. Eu., L. Cret. NA. As. Aus. SA., *Vinctifer* L. Cret. SA.

ORDER AMIOIDEA. **F. Caturidae (Eugnathidae),** *Allolepidotus Eoeugnathus* M.–U. Trias. Eu., *?Promecosomia* M.–U. Trias. Aus., *Brachichthys* [*Heterolepidotus*] M. Trias.–L. Jur. Eu., *Eugnathus* [*Furo Isopholis*] M. Trias.–U. Jur. Eu., Jur. As., *Dandya* [*Spaniolepis*] U. Trias. Eu., *Caturus* U. Trias.–L. Cret. Eu., *Osteorhachis* L.–U. Jur. Eu., *Ditaxiodus Eurycormus Strobilodus Thalattodus* U. Jur. Eu., *Callopterus* U. Jur.–L. Cret. Eu., *Otomitla* L. Cret. NA., *Neorhombolepis* L.–U. Cret. Eu., L. Cret. SA., *Lophiostomus* U. Cret. Eu. **F. Amiidae,** *Liodesmus* U. Jur. Eu., *Urocles* [*Megalurus*] U. Jur. Eu., L. Cret. SA., *Amiopsis* U. Jur.–L. Cret. Eu., ?Jur. NA., *Opsigonias* L. Cret. Eu., *Sinamia* L. Cret. As., *Kindleria Platacodon* U. Cret. NA., *?Stylomyleodon* U. Cret.–Paleoc. NA., *Protamia* Paleoc. Eu., Paleoc.–Eoc. NA., *Paramiatus* Eoc. NA., *Pappichthys* Eoc. NA. As., *Amia* Paleoc.–Mioc. Eu., Eoc.–R. NA. **F. Pachycormidae,** *Hypsocormus* U. Trias., M.–U. Jur. Eu., *Euthynotus Pachycormus Prosauropsis Saurostomus* L. Jur. Eu., *Sauropsis* L.–U. Jur. Eu., Jur. NA., *Asthenocormus ?Leedsichthys Orthocormus* U. Jur. Eu., *Eugnathides* Jur. NA., *Protosphyraena* [*Erisichthe Pelecopterus*] U. Cret. Eu. NA. SA. NAf. **F. Macrosemiidae,** *Ophiopsis* M. Trias.–L. Cret. Eu., *Legnonotus ?Orthurus* U. Trias. Eu., *Enchelyopsis* M. Jur. Eu., *Histionotus Macrosemius* M.–U. Trias. Eu., *Eusemius* U. Jur. NA., *Uarbryichthys* Jur. Aus., *Propterus Notagogus* U. Jur.–L. Cret. Eu., *Aphanepygus* L. Cret. Eu., *Macrepistius* L. Cret. NA., *Petalopteryx* L. Cret. Eu., U. Cret. WAs., *?Stromerichthys* U. Cret. NAf.

ORDER PHOLIDOPHOROIDEA. **F. Pholidophoridae,** *Prohalecites* M.–U. Trias. Eu., *Pholidophorus* M. Trias.–U. Jur. Eu., U. Trias. Af., L. Jur. NA., U. Jur. As. SA., *?Megalopterus* U. Trias. Eu., *Pholidophoroides* L. Jur. Eu., *Baleiichthys* Jur. NAs., *Ceramurus Pholidophoristion* U. Jur. Eu., *Ichthyokentema* U. Jur. Eu., Jur. NAs., *Pleuropholis* U. Jur.–L. Cret. Eu. **F. Archaeomaenidae,** *Archaeomaene* M. Trias.–Jur. Aus., *Aetheolepis Aphnelepis Madariscus* Jur. Aus. **F. Oligopleuridae,** *Oligopleurus Oeonoscopus* U. Jur.–L. Cret. Eu., *Calamoporus* Cret. SA., *Spathiurus* U. Cret. WAs.

SUPERORDER TELEOSTEI

ORDER ISOSPONDYLI

SUBORDER CLUPEOIDEA. **F. Leptolepidae,** *Leptolepis* ?Trias. L. Jur.–L. Cret. Eu., Jur. NA. Spitz. WAs., Jur.–L. Cret. SA., L. Cret. Af., *Vidalamia Eurystethus Ctenolepis* U. Jur. Eu., *Anaethalion* [*Aethalion*] *Thrissops Pachythrissops* U. Jur.–L. Cret. Eu., *Luisichthys* Jur. WInd., *Tharrhias Haplospondylus* L. Cret. SA., *Manchurichthys* L. Cret. As. **F. Lycopteridae,** *Lycoptera* L. Cret. As., *Neolycoptera* Jur.–Cret. SA. **F. Elopidae,** R. Oc., *Histialosa Hypsospondylus Hemielopopsis* L. Cret. Eu., *Rhacolepis Brannerion Calamopleurus ? Anaedopogon* L. Cret. SA., *Flindersichthys* L. Cret. Aus., *Elopopsis* L.–U. Cret. Eu., *Osmeroides* [*Holcolepis Rhabdolepis*] U. Cret. Eu. As. NA., *Spaniodon* U. Cret. WAs. NA., *Caeus Protelops Dinelops* U. Cret. Eu., *Thrissopater* U. Cret. Eu. NA., *Thrissopteroides* U. Cret. Eu. WAs., *Notelops Enneles Ennelichthys* U. Cret. SA., *Pachyrhizodus* U. Cret. Eu. NA., *Helmintholepis Oricardinus* U. Cret. NA., *Elops* U. Cret.–Eoc. Eu., U. Cret. SA. WAs., Mioc. NZ., R. Oc. *Esocelops* Eoc. Eu., *Megalops* Eoc. Eu., ?Mioc. NA., R. Oc., *Brouweria* Mioc. EInd., *Ectasis* Plioc. NA. **F. Albulidae,** R. Oc., *Hajulia* U. Cret. WAs., *Chanoides* Eoc. Eu., *Albula* [*Pisodus*] Paleoc.–Eoc. Eu., Eoc. NA. Af., R. Oc., *Paralbula* Mioc. NA. **F. Pterothrissidae,** R. Oc., *Istieus* U. Cret. Eu. WAs., *Chicolepis* Cret. NA., *? Ancylostylos* Cret. Eu. **F. Chirocentridae,** R. Oc., *Saurocephalus* L.–U. Cret. Eu., U. Cret. NA. NAf., *Chirocentrites Spathodactylus* L. Cret. Eu., *Chiromystus ?Cladocyclus* L. Cret. SA., *Sauro-*

don U. Cret. Eu. NA. NAf., *Andreiopleura* U. Cret. Eu., *Eubiodectes* U. Cret. WAs., ? *Anaedopogon* U. Cret. SA., *Proportheus* U. Cret. Af., *Prymnetes* U. Cret. NA., *Portheus* [*Hypsodon Xiphactinus*] U. Cret. NA. Eu. WAs. Aus. NZ. NAf., *Ichthyodectes* [*Gillicus*] U. Cret. Eu. NA. ?Aus., *Platinx* Eoc. Eu., *Chirocentrus* ?Tert. EInd., R. Oc. **F. Chanidae,** R. Oc., *Prochanos* L. Cret. Eu., *Dastilbe* L. Cret. SA., *Parachanos* L. Cret. Af., ? *Ancylostylos* U. Cret. Eu., *Chanos* Eoc.–Mioc. Eu., R. Oc. **F. Kneriidae Phractolaemidae Cromeriidae,** R. Af. **F. Clupeidae,** R. Cos., *Crossognathus* L. Cret. Eu., *Mesoclupea* L. Cret. EAs., *Scombroclupea* L. Cret. Eu., U. Cret. WAs. SA., *Apsopelix Leptichthys Paleoclupea Pelycorapis* U. Cret. NA., *Ellimmichthys* U. Cret. SA., *Histiothrissa* U. Cret. Eu., *Pseudoberyx* U. Cret. WAs., *Syllaemus* U. Cret. Eu. NA., *Diplomystus* [*Copeichthys Histiurus*] U. Cret. WAs. SA., Eoc. NA. Af. U. Cret.–Mioc. Eu., *Clupea* [*Sahelinia, Alosina*] Eoc.–Pleist. Eu., Olig. SA., Mioc. NA. EInd., Plioc. NAf., R. Oc., *Halecopsis* Eoc. Eu., *Knightia* Eoc. NA., *Neohalecopsis* Olig. Eu., *Meletta Melettina* Olig. Eu., *Alosa* Olig.–Plioc. Eu., Plioc. NAf., R. Oc., *Ganolytes* [*Diradias*] *Ganoëssus Xyne Opisthonema* Mioc. NA., *Caspialosa* Plioc.–R. WAs., *Brevoortia* Plioc. NAf., R. Oc., *Iquius* Tert. EAs. **F. Dussumieridae,** R. Oc., *Etrumeus* Olig. WAs., Mioc.–Plioc. Eu., Plioc. NAf., R. Oc., *Etringus* Mioc. NA., *Spratelloides* Plioc. NAf., R. Oc. **F. Bathyclupeidae,** R. Oc. **F. Engraulidae,** R. Oc., *Engraulis* Eoc.–Mioc. Eu., R. Oc. **F. Alepocephalidae Macristiidae,** R. Oc. **F. Ctenothrissidae,** *Ctenothrissa* U. Cret. Eu. WAs., *Aulolepis* U. Cret. Eu.

SUBORDER SALMONOIDEA. **F. Salmonidae,** R. Oc. Eu. As. NA., *Cyclolepis* ?*Leucichthyops* U. Cret. NA., *Thaumaturus* Eoc.–Mioc. Eu., *Salmo* ?Mioc., Plioc.–R. Eu., Pleist.–R. NA., R. Oc., *Rhabdofario* Plioc.–R. NA., *Cristivomer* Pleist.–R. NA., *Coregonus* Pleist.–R. Eu., R. NA. As., *Oncorhynchus* Pleist.–R. NA., R. Oc. **F. Thymallidae,** R. NA. Eu. As., *Protothymallus* Mioc. Eu. **F. Plecoglossidae,** R. As. **F. Osmeridae,** R. Oc., *Osmerus* Mioc. Eu., R. Oc., *Mallotus* Pleist. NA. Gr. Eu., R. Oc. **F. Salangidae,** R. As. **F. Retropinnidae,** R. Aus. **F. Aplochitonidae,** R. SA. Aus. **F. Galaxiidae,** R. SA. Af. Aus.

SUBORDER OPISTHOPROCTOIDEA. **F. Argentinidae,** R. Oc., *Argentina* Eoc. Eu., R. Oc. **F. Bathylagidae,** R. Oc., *Bathylagus* Mioc. NA., R. Oc., *Azalois Lygisma Sternbergia* Mioc. NA. **F. Macropinnidae Microstomidae Opisthoproctidae Winteriidae Xenophthalmichthyidae,** R. Oc.

SUBORDER OSTEOGLOSSOIDEA. **F. Osteoglossidae,** R. SA. Af., ?*Eurychir* Cret. NA., *Brychaetus* Eoc. Eu. NAf., *Phareodus* [*Dapedoglossus*] Eoc. NA. Olig. Aus., *Musperia* L. Tert. EInd., *Scleropages* Tert.–R. EInd., R. Aus. **F. Pantodontidae,** R. Af. **F. Plethodontidae,** *Plethodus* U. Cret. Eu. NAf., *Ananogmius* [*Anogmius*] U. Cret. NA. Eu., *Paranogmius* U. Cret. NAf., *Thryptodus Pseudothryptodus Martinichthys Syntegmodus* U. Cret. NA. **F. Hiodontidae,** R. NA. **F. Notopteridae,** R. Af. As. EInd., *Notopterus* L. Tert.–R. As. EInd., R. Af. **F. Mormyridae Gymnarchidae,** R. Af.

SUBORDER STOMIATOIDEA. **F. Enchodontidae,** *Halec* L.–U. Cret. Eu., U. Cret. WAs., *Saurorhamphus* L. Cret. Eu., *Cimolichthys* ?L. Cret. SA., U. Cret. Eu. NA. NAf., *Enchodus* U. Cret. Eu. NA. WAs., U. Cret.–Eoc. NAf., *Apateodus* U. Cret. Eu. NAf., *Eurypholis Pantopholis* U. Cret. WAs., *Palaeolycus Dipnolepis* U. Cret. Eu., *Halecodon* ?*Leptecodon* U. Cret. NA., ?*Prionolepis* U. Cret. Eu. WAs. **F. Tomognathidae,** *Tomognathus* U. Cret. Eu. **F. Chauliodontidae,** R. Oc., *Chauliodus* Mioc. NA., R. Oc. **F. Gonostomidae,** R. Oc., *Cyclothone* Mioc. NA., R. Oc. *Gonostoma Photichthys* Mioc. Eu., Plioc. NAf., R. Oc. **F. Sternoptychidae,** R., Oc., *Mrazecia* Olig. Eu., *Sternoptyx* Olig. Eu., R. Oc., *Argyropelecus* Mioc. NAf. As., R. Oc. **F. Stomiatidae Astronesthidae Melanostomidae Idiacanthidae**, R. Oc.

SUBORDER GONORHYNCHOIDEA. **F. Gonorhynchidae**, R. Oc., *Gonorhynchops* U. Cret. Eu., *Charitosomus* U. Cret. Eu. WAs., *Notogoneus* Eoc.–Olig. Eu., Eoc. NA., Olig. Aus., *Phalacropholis Colpopholis* Olig. Eu.

ORDER OSTARIOPHYSI

SUBORDER CYPRINOIDEA. **F. Characinidae**, R. NA. SA. Af., ?*Erythrinolepis* Cret. NA., *Procharacinus Prohydrocyon* Eoc. Eu., *Eobrycon Lignobrycon* Tert. SA., *Characilepis* Mioc. SA., *Alestes* Tert.–R. Af. **F. Gasteropelecidae Xiphostomidae Anostomidae Hemiodontidae Gymnotidae Electrophoridae Rhamphichthyidae Sternarchidae**, R. SA., **Citharinidae**, R. Af. **F. Catostomidae**, R. EAs. NA. SA., *Catostomus* Eoc.–R. As., Pleist.–R. NA., *Amyzon Catostomites* Mioc. NA., *Chasmistes* Pleist.–R. NA. **F. Cobitidae**, R. Eu. As. NAf. **F. Homalopteridae**, R. As. **F. Cyprinidae**, R. Eu. As. Af. NA., *Blicca* Paleoc.–R. Eu., *Chela* Eoc. Eu., R. As. EInd., *Barbus* Olig.–R. Eu., Mioc.–R. Af. As., U. Tert.–R. EInd., *Hemitrichas* Olig. Eu., *Leuciscus* Olig.–R. Eu., Mioc.–R. NA. As., R. Af., *Tinca* Olig.–R. Eu., *Nemachilus* Olig.–R. Eu., R. Af. As., *Scardinus* Olig.–R. Eu., *Paraleuciscus Soricidens* Mioc. Eu., *Rhodeus Aspius* Mioc.–R. Eu., *Alburnus* Mioc.–R. Eu., Plioc. WAs., *Cyprinus* Mioc.–R. Eu., Plioc.–R. As., *Gobio* Mioc.–R. Eu., R. As., *Cobitis* Mioc.–R. Eu., Pleist.–R. NA., R. As. *Pseudorasbora* Mioc.–R. As., *Carassius* Plioc.–R. As., R. Eu., *Hypophthalmichthys* Plioc.–R. EAs., *Rasbora Osteochilus Puntius* L. Tert.–R. EInd., *Eocyprinus* L. Tert. EInd., *Daunichthys Hexapsephus* Tert. EInd., *Thynnichthys Amblypharyngodon* Tert.–R. EInd., *Varicorhinus* U. Tert.–R. As., R. Af., *Diastichus Aphelichthys Alisodon* Pleist. NA., *Siphateles Notropis Ptychocheilus Mylopharodon* Pleist.–R. NA., *Ctenopharyngodon* Plioc.–R. As.

SUBORDER SILUROIDEA. **F. Diplomystidae**, R. SA. **F. Ariidae**, R. SA. Af. EInd. Oc., *Rhineastes* Eoc.–Olig. NA., Eoc.–R. As., *Felichthys* Mioc.–R. NA. **F. Doradidae**, R. SA. **F. Plotosidae**, R. EInd. **F. Siluridae**, R. Eu. As., *Silurus* Eoc.–R. Eu., R. As. **F. Ameiuridae**, R. NA., *Ameiurus* Olig.–R. NA. **F. Bagridae**, R. As. Af. EInd. *Bucklandium* Eoc. Eu., *Nigerium Eaglesomia* Eoc. Af., *Fajumia Socnopaea* Eoc. NAf., *Macrones* [*Macronoides*] Eoc. Af., R. As., *Aoria* Tert.–R. EInd., *Rita Macronichthys Heterobagrus* Plioc.–R. As., *Bagrus* Pleist.–R. Af. **F. Amblycipitidae**, R. As. **F. Sisoridae**, R. As., *Bagarius* Plioc.–R. As., Tert. EInd. **F. Amphiliidae**, R. Af. **F. Chacidae** R. As. **F. Schilbeidae**, R. Af. As. EInd., *Pangasius* L. Tert.–R. As., *Pseudeutropius* Tert.–R. EInd. **F. Clariidae**, R. As. Af., *Clarias* Plioc.–R. As. Af. **F. Mochocidae (Synodontidae)**, R. Af., *Synodontis* Mioc. Eu., Plioc.–R. Af. **F. Malapteruridae**, R. Af. **F. Helogenidae Hypophthalmidae**, R. SA. **F. Pimelodidae**, R. SA., *Pimelodus* Tert.–R. SA., ?Eoc. Af. **F. Trichomycteridae Bunocephalidae Loricariidae**, R. SA. **F. Callichthyidae**, R. SA., *Corydoras* U. Tert.–R. SA.

ORDER APODES. **F. Anguillavidae**, *Anguillavus* U. Cret. WAs. ?NA. **F. Urenchelyidae**, *Urenchelys* U. Cret. Eu. WAs. **F. Derichthyidae**, R. Oc., **F. Anguillidae**, R. Oc. Eu. NAf. NA. EAs. EInd., *Anguilla* ?Eoc. Eu., R. Eu. NAf. NA. As. Oc., *Mastygocercus* Mioc. EInd. **F. Simenchelyidae Synaphobranchidae Ilyophidae Dysommidae Xenocongridae Myrocongridae**, R. Oc. **F. Muraenesocidae**, R. Oc., *Muraenesox* Eoc. Eu., R. Oc. **F. Congridae**, R. Oc., *Congermuraena* Eoc. Eu., R. Oc., *Uroconger* Eoc. Eu., R. Oc., *Conger* Eoc. Eu., Mioc. NZ., R. Oc. **F. Nettastomidae**, R. Oc., *Nettastoma* ?Eoc. Eu., R. Oc. **F. Nessorhamphidae Heterocongridae**, R.

Oc. **F. Echelidae (Myridae)**, R. Oc., *Eomyrus Paranguilla Rhynchorhinus* Eoc. Eu., *Mylomyrus* Eoc. NAf., *Myrus* Eoc. Eu., R. Oc. **F. Nemichthyidae**, R. Oc., *Nemichthys* Eoc. Olig. WAs., R. Oc. **F. Cyemidae**, R. Oc. **F. Ophichthyidae**, R. Oc., *Ophichthys* Eoc. Eu., R. Oc., *Sphagebranchus* Mioc. Eu., R. Oc. **F. Neenchelyidae Moringuidae Heterenchelyidae**, R. Oc. **F. Muraenidae**, R. Oc., *?Deprandus* Mioc. NA., *Muraena* Plioc. NAf., R. Oc.

ORDER HETEROMI. **F. Notacanthidae**, R. Oc., *Pronotacanthus* U. Cret. WAs., Olig. Eu. **F. Halosauridae**, R. Oc., *Echidnocephalus* U. Cret. Eu. ?NA., *Enchelurus* U. Cret. Eu. WAs., *Laytonia* ?Cret. Mioc. NA., *Halosaurus* Mioc. NA., R. Oc. **F. Lipogenyidae**, R. Oc., **?F. Dercetidae**, *Dercetis Pelargorhynchus* U. Cret. Eu., *?Prionolepis* U. Cret. Eu. WAs., *Benthesikyme* [*Leptotrachelus*] U. Cret. Eu. WAs. NA., *Stratodus* U. Cret. NA., *?Palimphemus* Mioc. Eu. **?F. Blochiidae**, R. Oc., *Cylindracanthus* [*Coelorhynchus Glyptorhynchus*] U. Cret.–Olig. Eu., U. Cret. WAs., Eoc. Af. As. NA.

ORDER MESICHTHYS

SUBORDER HAPLOMI. **F. Esocidae**, R. Eu. NAs. NA., *Esox* Olig.–R. Eu., Tert.–R. As., R. NA. **F. Palaesocidae**, *Palaesox* Eoc. Eu. **F. Umbridae**, R. Eu. NA. **F. Dalliidae**, R. EAs. NA.

SUBORDER INIOMI (SCOPELOIDS). **F. Cheirothricidae**, *Cheirothrix Telepholis* U. Cret. Eu. WAs., *Exocoetoides* U. Cret. WAs. **F. Aulopidae**, R. Oc., *Sardinioides* U. Cret. Eu. WAs. **F. Synodontidae**, R. Oc., *Synodus* Mioc. Eu., Plioc. NAf., R. Oc. **F. Cetomimidae Scopelarchidae**, R. Oc. **F. Sudidae**, R. Oc., *Sudis* Mioc.–Plioc. Eu., Mioc. NAf., R. Oc., *Paralepis* Plioc. Eu. NAf., R. Oc. **F. Myctophidae (Scopelidae)**, R. Oc., *Nematonotus Opisthopteryx Hakelia* U. Cret. WAs., *Ichthyotringa* [*Rhinellus*] U. Cret. WAs. Eu. NA., *Hemisaurida Dactylopogon Tachynectes* U. Cret. Eu., *Sendhorstia* [*Microcoelia*] *Cassandra* [*Leptosomus*] *Acrognathus* U. Cret. WAs. Eu., *Sardinius* U. Cret. Eu. NA., *Omiodon Holosteus* Eoc. Eu., *Myctophum* [*Scopelus*] Eoc.–Plioc. Eu., Mioc. NZ., Plioc. NAf., R. Oc., *Scopeloides* Olig. Eu., *Parascopelus* Mioc. Eu., *Lampanyctus* Mioc. NA., Mioc.–Plioc. Eu., R. Oc., *Palimphemus* Mioc. Eu. **F. Omosudidae Alepisauridae Ateleopodidae Saccopharyngidae Eurypharyngidae**, R. Oc.

SUBORDER MICROCYPRINI. **F. Cyprinodontidae**, R. Eu. Gr. Af. NA. SA., *Prolebias* [*Ismene*] Olig.–Mioc. Eu., *Proballostomus* Olig. NA., *Haplochilus* Olig.–R. Eu., *Cyprinodon* L. Tert. SA., R. NA. As. Eu. NAf., *Carrionellus* L. Tert. SA., *Brachylebias* Mioc. WAs., *Pachylebias* Mioc. Eu., *Parafundulus* Mioc. NA., *Fundulus* Mioc.–R. Eu., Plioc.–R. NA., R. SA. As. Af., *Lithopoecilus* Tert. EInd. **F. Poeciliidae**, R. NA. SA. **F. Goodeidae Amblyopsidae**, R. NA. **F. Jenynsiidae Anablepidae**, R SA. **F. Phallostethidae**, R. As. **F. Adrianichthyidae**, R. EInd.

SUBORDER SYNENTOGNATHI. **F. Belonidae**, R. Oc., *Belone* Eoc.–Mioc. Eu., Mioc. NAf., R. Oc. **F. Scomberesocidae**, R. Oc., *Scomberesox* Mioc. Eu. NA., Plioc. NAf., R. Oc. **F. Hemirhamphidae**, R. Oc., *Cobitopsis* ?U. Cret. WAs., Olig. Eu., *Hemirhamphus* Eoc. Eu., R. Oc., *Euleptorhamphus* [*Beltion*] *Derrhias* Mioc. NA., R. Oc., *Rogenites Zelosus* Mioc. NA. **F. Exocoetidae**, R. Oc. **F. Forficiidae**, *Forfex Zelotichthys* Mioc. NA.

SUBORDER THORACOSTEI. **F. Gasterosteidae**, R. Eu. As. NAf. NA., *Gasterosteops* U. Tert. As. Af., *Gasterosteus* Mioc.–R. NA., R. Eu. Af. As. **F. Aulorhynchidae**, R. Oc., *Protaulopsis* Eoc. Eu., *Aulorhynchus* Tert. EInd., R. Oc., *Protosyngnathus* Tert. EInd. **F. Macrorhamphosidae**, R. Oc. **F. Centriscidae**, R. Oc., *?Aulorhamphus* [*Amphisyle*] Olig. Eu., R. Oc., *Centriscus* ?Plioc. Eu., R. Oc. **F. Aulostomi-**

dae, R. Oc., *Urosphen* Eoc. Eu., *Aulostoma* Eoc.–Olig. Eu., R. Oc. **F. Fistulariidae,** R. Oc., *Fistularia* Olig.–Plioc. Eu., R. Oc. **F. Solenostomidae,** R. Oc., *Solenorhynchus, Solenostomus* Eoc. Eu., R. Oc., *Siphonostoma* Mioc. Eu., R. Oc. **F. Syngnathidae,** R. Oc., *Calamostoma Pseudosyngnathus* Eoc. Eu., *Syngnathus* Mioc. NA., Plioc. NAf., R. Oc. **?F. Pegasidae,** R. Oc. **?F. Indostomidae,** R. As.

SUBORDER SALMOPERCAE. **F. Aphreoderidae,** R. NA., *Erismatopterus Amphiplaga Asineops* Eoc. NA., *Trichophanes* Mioc. NA. **F. Percopsidae,** R. NA.

ORDER ACANTHOPTERYGII

SUBORDER BERYCOIDEA. **F. Polymixiidae,** R. Oc., *Pycnosterinx Pycnosteroides Omosoma* U. Cret. WAs., *Platycormus* U. Cret. Eu., *Polymixia* Eoc. Eu., R. Oc. **F. Berycopsidae,** *Berycopsis* U. Cret. Eu. **F. Berycidae,** R. Oc., *Hoplopteryx Kansius* U. Cret. Eu. NA., *Beryx* Eoc. Eu., Olig. WAs., R. Oc., *Africentrum* [*Microcentrum*] Mioc. Eu., Plioc. NAf., R. Oc. **F. Diretmidae Anomalopidae,** R. Oc. **F. Monocentridae,** R. Oc., *Monocentris* Eoc. Eu. Aus., R. Oc. **F. Trachichthyidae,** R. Oc., *Acrogaster Aipichthys* U. Cret. Eu. WAs., *Sphenocephalus* U. Cret. Eu. **F. Holocentridae,** R. Oc., *Homonotichthys* [*Homonotus*] *Caproberyx Trachichthyoides* U. Cret. Eu., *Holocentrum* Eoc.–Mioc. Eu., R. Oc., *Myripristis* Eoc. Olig. Eu., R. Oc., *Holocentroides* Olig. Eu. **F. Dinopterygidae,** *Dinopteryx* U. Cret. WAs. **F. Caristiidae,** R. Oc., *Absalomichthys* [*Abantis*] *Chalcidichthys* Mioc. NA. **F. Stephanoberycidae ?Kurtidae Rondeletiidae,** R. Oc.

SUBORDER ZEOIDEA. **F. Palaeocentrotidae,** *Palaeocentrotus* Paleoc. Eu. **F. Zeidae,** R. Oc., *Cyttoides* Olig. Eu., *Zeus* Olig.–Plioc. Eu., ?Plioc. NAf. **F. Grammicolepidae,** R. Oc. **F. Caproidae,** R. Oc., *Capros* [*Proantigonia*] Olig.–Mioc. Eu., Plioc. NAf., R. Oc.

SUBORDER PERCOIDEA. **F. Percidae,** R. Eu. As. NA., *Anthracoperca* Eoc. Eu., *Mioplosus* Eoc. NA., *Perca* Eoc.–R. Eu., R. NA., *Propercarina Podocys Pachygaster* Olig. Eu., *Eoperca* Olig. NA., *Percichthys* Tert.–R. SA., *Lucioperca* Pleist.–R. Eu. **F. Apogonidae,** R. Oc., *Apogon* Eoc.–Mioc. Eu., R. Oc., *Apogonoides* Plioc. NAf., R. Oc. **F. Scombropidae Acropomatidae,** R. Oc. **F. Centrarchidae,** R. NA., *Centrarchites* Eoc. NA., ?*Parapygaeus* Eoc. Eu., *Oligoplarchus* Olig. NA., *Mioplarchus Boreocentrarchus* Mioc. NA., *Micropterus* Mioc.–R. NA., *Chaenobryttus Pomoxis* Plioc.–R. NA., *Catostomites* Tert.–R. NA., *Lepomis* Pleist.–R. NA. **F. Kuhliidae,** R. Oc. As. EInd. **F. Centropomidae,** R. Oc., *Prolates* U. Cret.–Paleoc. Eu., *Centropomus* Eoc.–R. Eu., R. NA., *Lates* Eoc.–R. NAf., Eoc. Eu., R. As. Aus., *Platylates Paralates* Olig. Eu. **F. Serranidae,** R. Cos., *Properca* Eoc.–Mioc. Eu., *Amphiperca Serranus* Eoc.–Mioc. Eu., Plioc. NAf., R. Oc., *Labrax* Eoc.–Plioc. Eu., R. Oc., *Smerdis* Eoc.–Mioc. Eu., ?Eoc. NAf., *Cyclopoma* Eoc. Eu., *Percilia* Eoc. Eu., R. SA., *Percalates* Olig.–R. Aus., *Acanus* Olig. Eu., *Niphon* Olig. Eu., R. Oc., *Emmachaere Protanthias* Mioc. NA., *Epinephelus* Mioc. NA., Plioc. NAf., R. Oc., *Anthias* Mioc. Eu., R. Oc., *Eoserranus* Tert. As. **F. Priacanthidae,** R. Oc., *Pristigenys* Eoc. Eu., *Priacanthus* Olig. Eu., R. Oc. **F. Plesiophidae Acanthoclinidae Pseudoplesiopidae Pempheridae Lobotidae Glaucosomidae Arripidae,** R. Oc. **F. Lutianidae,** R. Oc., *Lutianus* ?Eoc. Eu., Olig. NA., R. Oc. **F. Pomadasyidae (Pristipomidae),** R. Oc., *Pomadasys* Eoc. NAf., R. Oc., *Orthopristis Parapristopoma* Plioc. NAf., R. Oc. **F. Therapomidae Banjosidae Lethrinidae Neolethrinidae,** R. Oc. **F. Sparidae,** R. Oc., *Chrysophrys* Paleoc.–Mioc. Eu., R. Oc., *Pagellus* Paleoc.–Mioc. Eu., Olig.–Mioc. NZ., Plioc. NAf., R. Oc., *Dentex* Eoc.–Plioc. Eu., Mioc. NZ., Plioc. NAf., R. Oc., *Sparnodus* Eoc.–Mioc. Eu., *Diplodus Crenidens* Plioc. NAf., R. Oc., *Smaris Spondyliosoma* [*Cantharus*] Eoc.

Eu., R. Oc., *Pagrus* Eoc.–Plioc. Eu., Plioc. NAf., R. Oc., *Ctenodentex* Eoc. Eu. NAf., *Sargus* Eoc.–Plioc. Eu., ?Eoc., Mioc. NAf., R. Oc., *Rhythmias ?Crommyodus Plectrites* Mioc. NA., *Sparus* Mioc.–Plioc. Eu., Plioc. NAf., R. Oc., *Paracalamus* Plioc. NAf. **F. Girellidae,** R. Oc., *Box* Mioc. Eu., Plioc. NAf., R. Oc. **F. Enoplosidae,** R. Oc., *Enoplosus* Eoc. Eu., R. Oc. **F. Cyphosidae Histiopteridae Inermiidae,** R. Oc. **F. Maenidae,** R. Oc., *Maena* Plioc. NAf., R. Oc. **F. Emmelichthyidae Hoplegnathidae Mullidae,** R. Oc. **F. Sciaenidae (Otolithidae),** R. Oc., *Otolithus* Eoc. Eu., R. Oc., *Diaphyodus* Eoc. Eu., *Sciaena* Olig.–Mioc. Eu., Olig. NA., R. Oc., *Pogonias* Mioc.–Pleist. NA., R. Oc., *Lompoquia* Mioc. NA., *Cynoscion* Mioc. NA., R. Oc., *Umbrina* Plioc. Eu., R. Oc. **F. Sillaginidae Nandidae Polycentridae Malacanthidae Labracoglossidae,** R. Oc. **F. Latilidae** R. Oc., *Pateroperca* U. Cret. WAs., *Latilus* Plioc. NAf., R. Oc. **F. Cepolidae,** R. Oc., *Cepola* Eoc. Eu., Plioc. NAf., R. Oc. **F. Cirrhitidae Chironemidae Haplodactylidae Latridae,** R. Oc. **F. Gadopsidae,** R. Aus. **F. Embiotocidae,** R. Oc., *Ditrema* Eoc. Eu., R. Oc., *Eriquius* Mioc. NA. **F. Pomacentridae,** R. Oc., *Priscacara Cockerellites* Eoc. NA., *Odonteus* Eoc. Eu., *Izuus* Mioc. EAs. **F. Cichlidae,** R. CA. SA. WInd. Af. SAs., *Macracara* Eoc. SA., *Palaeochromis* Tert. NAf., *Chromis* Mioc.-R. Af., *Cichlasoma* Mioc. WInd., R. SA., *Acara* Tert.–R. SA., *Tilapia* Tert.-R. Af., R. WAs. **F. Scaridae,** R. Oc., *Scarus* [*Callyodon*] Eoc. Eu., Mioc. SAs., R. Oc., *Pseudoscarus* Eoc. Eu., R. NA. SA. As., *Taurinichthys* Mioc. Eu., *Scaroides* Tert. CA. **F. Odacidae,** R. Aus. NZ. **F. Labridae,** R. Oc., *Phyllodus* U. Cret.–Eoc. NA., Eoc. NAf., Eoc.–Mioc. Eu., *Labrodon* Eoc. Af. NZ., Eoc.–Plioc. Eu., Mioc. As. NA., R. Oc., *Egertonia Platylaemus* Eoc. Eu. NAf., *Pseudosphaerodon Gillidia Eolabroides* Eoc. Eu., *Labrus* Eoc.–Plioc. Eu., R. Oc., *?Crommyodus Protautoga* Mioc. NA., *Stylodus* Mioc. Eu., *Julis* Mioc. Eu., R. Oc., *Crenilabrus* Plioc. NAf., Tert. Eu., R. Oc.

SUBORDER CARANGOIDEA. **F. Bramidae,** R. Oc., *Protobrama* U. Cret. WAs. **F. Coryphaenidae Steinegeriidae Pteraclidae Stromateidae Tetragonuridae Icosteidae Formionidae,** R. Oc. **F. Nomeidae,** R. Oc., *Carangodes* Eoc. Eu. **F. Carangidae,** R. Oc., *Aipichthys* Cret. Eu., U. Cret. WAs., *Teratichthys Carangopsis Ductor Vomeropsis* Eoc. Eu., *Acanthonemus* Eoc.-Olig. Eu., *Trachurus* Eoc. Eu., Plioc. NAf., R. Oc., *Seriola* Eoc.–Olig. Eu., Mioc. NA., Plioc. NAf., R. Oc., *Caranx* [*Parequula*] Eoc.–Plioc. Eu., Plioc. NAf., Pleist. NA., R. Oc., *Archaeus* Olig. Eu., *Lichia* Olig.–Pleist. Eu., R. Oc., *Lompochites* Mioc. NA., *Pseudovomer* Mioc. Eu., *Decapterus* Mioc. NA., Plioc. NAf., R. Oc., *Equula Vomer Trachinotus* Tert. Eu., R. Oc. **F. Ioscionidae,** R. Oc., *Ioscion* Mioc. NA., R. Oc. **F. Nematistiidae,** R. Oc. **F. Menidae,** R. Oc., *Mene* [*Gasteracanthus*] Eoc. Eu., Plioc. NAf. WInd., R. Oc. **F. Pomatomidae,** R. Oc., *Lophar Pseudoseriola* Mioc. NA. **F. Rachycentridae Lactariidae Liognathidae,** R. Oc.

SUBORDER SCOMBROIDEA. **F. Scombridae,** R. Oc., *Xiphopterus Scombrinus Eocoelopoma Ardiodus* Eoc. Eu., *Sphyraenodus* Eoc. Af., Eoc.–Mioc. Eu., *Scombramphodon* Eoc.–Olig. Eu., *Gymnosarda* Eoc.–Olig. Eu., R. Oc., *Cybium* Eoc.-Mioc. Eu., Olig. SA. WAs., R. Oc., *Auxis* Eoc.–Mioc. Eu., R. Oc., *Scomber* Eoc.–Plioc. Eu., Mioc. NA., Plioc. NAf., Tert. EAs., R. Oc., *Palimphyes Palaeoscomber Megalolepis* Olig. Eu., *Isurichthys* Olig. Eu. WAs., *Neocybium* Olig.–Mioc. Eu., *Stereodus* Mioc. Eu., *Pneumatophorus* Mioc. Eu. NA., Plioc. NAf., R. Oc., *Ocystias* Mioc. NA. **F. Thunnidae,** R. Oc., *Sarda* [*Pelamys*] Paleoc.–Eoc. Eu., Plioc. NAf., R. Oc., *Eothynnus* Eoc. Eu., Plioc. NAf., R. Oc., *Thunnus* Eoc.–Pleist. Eu., Mioc. NA. Af., *Ozymandias* Mioc. NA. **F. Palaeorhynchidae,** *Homorhynchus* [*Hemirhynchus*] Eoc.–Olig. Eu., *Palaeorhynchus* Eoc.–Mioc. Eu., Olig. WAs. **F. Histiophoridae,** R. Oc., *Histiophorus* U. Cret.–Mioc. NA., Eoc.–Plioc. Eu., R. Oc., *Tetraptu-*

rus Eoc. Eu., R. Oc. **F. Xiphiidae,** R. Oc., *Acestrus* Eoc. Eu., *Xiphias* Eoc.–Olig. Eu., Pleist. NA., R. Oc. **F. Xiphiorhynchidae,** *Xiphiorhynchus* [*Ommatolampes*] Eoc. Eu., Eoc.–Plioc. NAf. **F. Luvaridae,** R. Oc. **F. Trichiuridae,** R. Oc., *Trichiurides* Paleoc.–Mioc. Eu., Eoc. Af., *Lepidopus* Olig. SA., Olig.–Plioc. Eu., Plioc. NAf., *Trichiurus* Eoc. Af., Pleist. NA., R. Oc. **F. Gempylidae,** R. Oc., *Bathysoma* U. Cret. Eu., *Eothyrsites* Olig. NZ., *Thyrsitocephalus* Olig. Eu., *Gempylus* Olig. WAs., R. Oc., *Thyrsites* Mioc. NA., R. Oc., *Hemithyrsites* Plioc. Eu. **F. Euzaphlegidae,** *Euzaphleges* [*Zaphleges*] *Thyrsocles Zaphlegulus* Mioc. NA.

SUBORDER TRACHINOIDEA. **F. Trachinidae,** R. Oc., *Callipteryx* Eoc. Eu., *Trachinus* Eoc.–Mioc. Eu., R. Oc., *Trachinopsis* Plioc. Eu. **F. Nototheniidae Bathydraconidae Channichthyidae,** R. Oc. **F. Bovichthyidae,** R. Oc. Aus. **F. Draconettidae,** R. Oc. **F. Callionymidae,** R. Oc., *Callionymus* Mioc. Eu., R. Oc. **F. Percophididae Mugiloididae Bembropsidae Hemerocoetidae Creediidae Limnichthyidae Trichonotidae Oxudercidae Bathymasteridae,** R. Oc. **F. Chimarrhichthyidae** R. NZ. **F. Zaproridae,** R. Oc., *Aracosteus* Mioc. NA. **F. Chiasmodontidae Opisthognathidae Owstoniidae Champsodontidae,** R. Oc. **F. Uranoscopidae,** R. Oc., *Uranoscopus* Eoc. Eu., R. Oc. **F. Leptoscopidae,** R. Oc., *Neopercis* Plioc. NAf., R. Oc. **F. Dactyloscopidae Trichodontidae** R. Oc.

SUBORDER BLENNIOIDEA. **F. Clinidae,** R. Oc., *Pterygocephalus* Eoc. Eu., *Clinus* Mioc. Eu., Plioc. NAf., R. Oc. **F. Notograptidae Peronedyidae Ophioclinidae,** R. Oc. **F. Blenniidae,** R. Cos., *Oncolepis* Eoc. Eu., *Problennius* Eoc. WAs., *Blennius* Mioc. Eu., R. Oc., *Tripterygion* Plioc. NAf., R. Oc. **F. Pholidae Xiphisteridae,** R. Oc. **F. Stichaeidae,** R. Oc., *Stichaeus* Tert. EAs., R. Oc. **F. Lumpenidae Ptilichthyidae,** R. Oc. **F. Anarhichadidae,** R. Oc., *Anarhichas* Plioc. Eu., R. Oc. **F. Xenocephalidae Congrogadidae Scytalinidae Zoarcidae Lycodapodidae Derepodichthyidae,** R. Oc. **F. Ophidiidae,** R. Oc., *Ophidium* ?Paleoc. Eoc.–Mioc. Eu., R. Oc. **F. Brotulidae,** R. Oc., *Brotula* ?Mioc. Eu., R. Oc. **F. Fierasferidae,** R. Oc., *Fierasfer* Olig.–Mioc. NZ., R. Oc.

SUBORDER ANACANTHINI. **F. Macrouroididae,** R. Oc. **F. Macrouridae,** R. Oc., *Macrourus* Eoc.–Mioc. Eu., Mioc. NA. NZ., R. Oc., *Bolbocara* Mioc. NA., *Trichiurichthys* Mioc.–Plioc. Eu. **F. Bregmacerotidae,** R. Oc., *Bregmaceros* Eoc.–Plioc. Eu., ?Eoc. NZ., Olig. WAs., Plioc. NAf., R. Oc. **F. Gadidae,** R. Oc., *Gadus* Paleoc.–Pleist. Eu., R. Oc., *Merluccius* Eoc.–Mioc. Eu., Mioc. NZ., R. Oc., *Phycis Neobythites* Eoc. Eu., R. Oc., *Palaeogadus* [*Nemopteryx*] Olig. Eu., *Brosmius* Olig.–Plioc. Eu., Plioc. NAf., R. Oc., *Eclipes* Mioc. NA., *Onobrosmius* Mioc. WAs., *Physiculus* Mioc. NZ., R. Oc., *Lota* Plioc.–R. Eu., R. As. NA., *Arnoldites* Plioc. NA. **F. Muraenolepidae,** R. Oc.

SUBORDER CHAETODONTOIDEA. **F. Scorpidae,** R. Oc. **F. Amphistiidae,** *Amphistium* [*Macrostoma*] Eoc.–Olig. Eu. **F. Ephippidae,** R. Oc., *Ephippus* Eoc. Eu., Pleist. NA., R. Oc., *Platax* Eoc.–Plioc. Eu., Plioc. NA., R. Oc., *Semiophorus* [*Exellia*] Eoc. Eu., *Ephippites* Olig. Eu. **F. Drepanidae,** R. Oc. **F. Toxotidae,** R. Oc. EInd., *Toxotes* L. Tert.–R. EInd. **F. Scatophagidae,** R. Oc. *Scatophagus* Eoc.–Mioc. Eu., R. Oc. **F. Chaetodontidae,** R. Oc. *Holacanthus* Eoc.–Mioc. Eu., R. Oc., *Chaetodon* Olig.–Mioc. Eu., Plioc. NAf., R. Oc., *Chelmon* Mioc. EInd., R. Oc.

SUBORDER PLECTOGNATHI (BALISTOIDEA)

INFRAORDER TEUTHIDOIDEA. **F. Zanclidae,** R. Oc., *Zanclus* Eoc. Eu., R. Oc. **F. Acanthuridae,** R. Oc., ?*Aulorhamphus* Eoc. Eu., *Naseus* Eoc. Eu., R. Oc., *Acanthurus* Eoc.–Mioc. Eu., R. Oc., *Apostasis* Olig.–Mioc. Eu., *Zebrasoma* Tert. WInd., R. Oc. **F. Teuthidae (Siganidae),** R. Oc., *Pygaeus* ?*Parapygaeus* Eoc. Eu., *Archaeoteuthis* Olig. Eu.

INFRAORDER SCLERODERMI. **F. Eotrigonodontidae,** *Pharmacichthys* U. Cret. WAs., *Stephanodus* U. Cret. Eu. NA. Af., *Eotrigonodon* Eoc. Eu. Af. **F. Spinacanthidae,** *Spinacanthus* [*Protobalistum*] Eoc. Eu. **F. Trigonodontidae,** R. Oc., *Trigonodon* Eoc.–Plioc. Eu., Mioc. NZ., Plioc. NAf., R. Oc. **F. Triacanthidae,** R. Oc., *Triacanthus Pristigenys* [*Pseudotriacanthus*] Eoc. NAf., R. Oc., *Acanthopleurus* Eoc.–Olig. Eu. **F. Balistidae,** R. Oc., *Acanthoderma* Olig. Eu., *Marosia* Mioc. EInd., *Balistes* Plioc. NAf. EInd. Eu., R. Oc. **F. Ostraciidae,** R. Oc., *Ostracion* Eoc.–Olig. Eu., Tert. WInd., R. Oc. **F. Triodontidae,** R. Oc., *Triodon* Eoc. Eu. Af., R. Oc. **F. Tetraodontidae,** R. Oc., *Tetraodon* Eoc.–Plioc. Eu., R. Oc. **F. Diodontidae,** R. Oc., *Diodon* [*Chilomycterus*] Eoc.–Plioc. Eu. NAf. As., Eoc.–Pleist. NA., R. Oc. **F. Molidae,** R. Oc., *Mola* Plioc. Eu., Tert. SA., R. Oc.

SUBORDER HETEROSOMATA. **F. Psettodidae,** R. Oc., *Joleaudichthys* Eoc. NAf. **F. Bothidae,** R. Oc., *Eobothus* Eoc. ?Olig. Eu., Eoc. As., *Bothus* Eoc. Eu., R. Oc., *Rhombus* Eoc.–Plioc. Eu., R. Oc., *Citharichthys* Olig. Eu., Plioc. NAf., R. Oc., *Paralichthys* Mioc. NA., R. Oc., *Evesthes* Mioc. NA. **F. Pleuronectidae,** R. Oc., *Hippoglossoides* Mioc. NA., R. Oc., *Pleuronichthys* Mioc. NA., Plioc. Eu., R. Oc., *Protopsetta* Tert. EAs., R. Oc. **F. Soleidae,** R. Oc., *Solea* Paleoc.–Mioc. Eu., Eoc.–Plioc. NAf., R. Oc., *Turahbuglossus Eubuglossus* Eoc. NAf., *Microchirus* Mioc. Eu., Plioc. NAf., R. Oc., *Achirus* Plioc. NAf., R. Oc. **F. Cynoglossidae,** R. Oc.

SUBORDER SCORPAENOIDEA (SCLEROPAREI). **F. Scorpaenidae,** R. Oc., *Ampheristus* Eoc. Eu., *Scorpaenoides* Eoc.–Olig. Eu., *Scorpaena* Olig.–Mioc. Eu., Mioc. NA., Plioc. NAf., R. Oc., *Ctenopoma Scorpaenopterus* Mioc. Eu., *Sebastodes* Mioc.–Plioc. NA., Tert. EAs., R. Oc. **F. Congiopodidae,** R. SA. Af. Aus. **F. Aploactidae Synancejidae Caracanthidae Pataecidae,** R. Oc. **F. Anoplopomidae,** R. Oc., *Aneoscorpius* [*Eoscorpius*] Mioc. NA. **F. Hexagrammidae,** *Achrestogrammus* Mioc. NA. **F. Hoplichthyidae Platycephalidae,** R. Oc. **F. Icelidae,** R. Oc., *Paraperca* Olig. Eu. **F. Cottidae,** R. As. NA. Oc., *Eocottus* Eoc. Eu., *Cottopsis* Eoc. WAs., *Cottus* Eoc.–R. As., Mioc. NZ., Pleist.–R. NA., R. Eu., *Lepidocottus* Olig.–Mioc. Eu., *Lirosceles Hayia* Mioc. NA. **F. Psychrolutidae Ereuniidae,** R. Oc. **F. Cottocomephoridae Comephoridae,** R. As. **F. Agonidae,** R. Oc., *Agonus* Eoc. Eu., R. Oc. **F. Cyclopteridae,** R. Oc. *Cyclopterus* Pleist. NA., R. Oc. **F. Triglidae,** R. Oc. *Trigla* Eoc.–Mioc. Eu., Plioc. NAf., Pleist. NA., R. Oc., *Podopteryx* Mioc. Eu. **F. Dactylopteridae,** R. Oc.

SUBORDER BATRACHOIDEA (HAPLODOCI). **F. Batrachoididae,** R. Oc., *Batrachoides* Plioc. NAf., R. Oc.

SUBORDER PEDICULATI (LOPHIOIDEA). **F. Lophiidae,** R. Oc., *Lophius* Plioc. NAf., R. Oc. **F. Antennariidae,** R. Oc., *Histionotopterus* Eoc. Eu. **F. Brachionichthyidae Chaunacidae Ceratiidae Himantolophidae Melanocetidae Caulophrynidae Linophrynidae Gigantactinidae Diceratiidae Oneirodidae Laevoceratiidae Neoceratiidae,** R. Oc.

SUBORDER GOBIOIDEA. **F. Eleotridae,** R. Oc. SA. **F. Gobiidae,** R. Cos., *Gobiopsis* Eoc. WAs., R. Oc., *Gobius* ?Eoc., Olig.–Plioc. Eu., Plioc. NAf., R. Oc. **F. Periophthalmidae,** R. Oc.

SUBORDER ANABANTOIDEA (LABYRINTHICI). **F. Anabantidae,** R. Af., *Osphronemus* L. Tert. EInd., R. As. **F. Ophiocephalidae,** R. As. Af., *Ophiocephalus* Plioc.–R. As., R. Af. **F. Luciocephalidae,** R. EInd.

SUBORDER MUGILOIDEA (PERCESOCES). **F. Mugilidae,** R. Oc., *Mugil* Eoc.–Plioc. Eu., Plioc. NAf., R. Oc. **F. Sphyraenidae,** R. Oc., *Sphyraena* Eoc.–Mioc. Eu., Eoc. Af., Mioc. EInd., Pleist. NA., R. Oc. **F. Atherinidae,** R. NA. Aus. Oc., *Rhamphog-*

nathus Eoc. Eu., *Atherina* Eoc.–R. Eu., Mioc.–R. As., R. NA., *Menidia* Plioc.–R. NA.

SUBORDER POLYNEMOIDEA. F. **Polynemidae,** R. Oc.

SUBORDER AMMODYTOIDEA. F. **Ammodytidae,** R. Oc., *Ammodytes* Olig. Eu., R. Oc. ?F. **Rhamphosidae,** *Rhamphosus* Eoc. Eu.

SUBORDER ECHENEOIDEA. F. **Echeneidae,** R. Oc., *Echeneis* Olig. Eu., R. Oc., *Opisthomyzon* Olig. Eu.

SUBORDER XENOPTERYGII. F. **Gobiesocidae,** R. Oc., *Bulbiceps* Mioc. NA.

SUBORDER ALLOTRIOGNATHI. F. **Lampridae,** R. Oc., *Lampris* Mioc. NA., R. Oc. F. **Lophotidae,** R. Oc., *Lophotes* Olig. WAs., R. Oc. F. **Veliferidae Regalecidae Trachipteridae,** R. Oc.

SUBORDER OPISTHOMI. F. **Mastacembelidae,** R. Af. As. F. **Chaudhuriidae,** R. As.

SUBORDER SYNBRANCHII. F. **Synbranchidae,** R. SA. Af. As. EInd. F. **Amphipnoidae,** R. As. Aus. F. **Alabetidae,** R. Aus.

SUBCLASS CHOANICHTHYES

ORDER CROSSOPTERYGII

SUBORDER RHIPIDISTIA (OSTEOLEPIDOTI). F. **Porolepidae,** *Porolepis* L.–M. Dev. Eu. Spitz. NAs. F. **Osteolepidae,** *Canningius* M. Dev. Gr., *Diplopterax* [*Diplopterus*] M. Dev. Eu. Gr., *Gyroptychius Tristichopterus* M. Dev. Eu., *Osteolepis* M.–U. Dev. Eu., Dev. NAs. Ant., *Thursius* M. Dev. Eu., U. Dev. NA., ?*Devonosteus Polyplocodus* M.–U. Dev. Eu., *Eusthenopteron Glyptopomus Sauripterus* U. Dev. Eu. NA., *Dictyonosteus* U. Dev. Spitz., *Thaumatolepis* Dev. Eu., *Megalichthys* [*Rhizodopsis*] ?U. Dev. NAs., Penn. ?Perm. Eu., Penn. NA., *Rhizodus* Miss. Eu. ?NA., *Strepsodus* Miss.–Penn. Eu. NA., Penn. Aus., *Ectosteorhachis* L. Perm. NA. F. **Holoptychiidae,** *Hamodus* M. Dev. Eu., *Glyptolepis* M.–U. Dev. Eu., U. Dev. NA. NAs., *Holoptychius* [*Dendrodus*] U. Dev. Eu. NA. Gr. Ant. ?NAs.

SUBORDER COELACANTHINI (ACTINISTIA). F. **Diplocercididae,** *Euporosteus* M. Dev. Eu., *Diplocercides Nesides* U. Dev. Eu. F. **Coelacanthidae,** ?*Coelacanthopsis* Miss. Eu., *Rhabdoderma* Miss.–Penn. Eu. NA., *Coelacanthus* Penn.–U. Perm. Eu., ?Perm. Mad., *Spermatodus* L. Perm. NA., *Axelia Mylacanthus Scleracanthus* L. Trias. Spitz., *Sassenia* L. Trias. Spitz. Gr., *Wimania* [*Leioderma*] L. Trias. Spitz. ?Gr., *Whiteia* L. Trias. Mad. Gr., *Heptanema* M.–U. Trias. Eu., *Diplurus Osteopleurus* U. Trias. NA., *Graphiurichthys* [*Graphiurus*] U. Trias. Eu., *Undina* U. Trias.–Jur. Eu., ?Jur. Aus. *Trachymetopon* L. Jur. Eu., *Coccoderma Libys* U. Jur. Eu., *Mawsonia* L. Cret. SA., U. Cret. NAf., *Macropoma* U. Cret. Eu. WAs., *Macrorhomboides* U. Cret. WAs., ?*Stromerichthys* U. Cret. Eu. F. **Laugiidae,** *Laugia* L. Trias. Gr. F. **Latimeriidae,** R. Oc.

ORDER DIPNOI. F. **Dipteridae,** *Dipnorhynchus* M. Dev. Aus., *Dipterus* M. Dev. Eu., M.–U. Dev. NA. Nova Zembla, *Pentlandia* M. Dev. Eu., *Ganorhynchus* M.–U. Dev. Eu. NA., *Conchodus* M.–U. Dev. Eu., U. Dev. NA., *Palaedaphus* U. Dev. Eu. NA., *Dipteroides Holodipterus* [*Holodus*] *Chirodipterus* U. Dev. Eu., *Rhynchodipterus* U. Dev. Eu. Gr., *Eoctenodus* U. Dev. Aus., *Synthetodus* U. Dev. NA. F. **Phaneropleuridae,** *Fleurantia Scaumenacia* U. Dev. NA., *Phaneropleuron* U. Dev. Eu. Gr. F. **Ctenodontidae,** *Uronemus* Miss. Eu., *Ctenodus* Miss.–Penn. Eu. NA., *Sagenodus* Miss.–Penn. Eu., Miss.–L. Perm. NA. F. **Conchopomidae,** *Conchopoma* [*Peplorhina*] Penn.–L. Perm. NA. F. **Ceratodontidae,** R. Aus., *Proceratodus* Penn.–L. Perm. NA., *Gosfordia* L. Trias. Aus., *Ceratodus* L. Trias.–U. Jur. Eu.,

L. Trias.–U. Cret. Aus. Af. NA., U. Trias.–L. Cret. As., U. Cret. SA., *Ptychoceratodus* U. Trias. Eu., *Epiceratodus* U. Cret.–R. Aus. **F. Lepidosirenidae,** R. Af. SA., ?*Gnathorhiza* Penn.–L. Perm. NA., U. Perm. Eu., *Protopterus* Olig.–R. Af.

CLASS AMPHIBIA

SUBCLASS APSIDOSPONDYLI

SUPERORDER LABYRINTHODONTIA

ORDER ICHTHYOSTEGALIA. ?**F. Elpistostegidae,** *Elpistostege* U. Dev. NA. **F. Ichthyostegidae,** *Ichthyostega Ichthyostegopsis* U. Dev. or Miss. Gr. **F. Otocratiidae,** *Otocratia* Miss. Eu. **F. Colosteidae,** *Colosteus Erpetosaurus* Penn. NA.

ORDER RHACHITOMI

SUBORDER LOXOMMOIDEA. **F. Loxommidae,** *Loxomma* Miss.–Penn. Eu., *Spathiocephalus* Miss. Eu., *Macrerpeton* Penn. NA., *Baphetes Megalocephalus* [*Orthosaurus*] Penn. Eu. NA.

SUBORDER EDOPSOIDEA. **F. Edopsidae,** *Leptophractus* Penn. NA., *Capetus Cochleosaurus Gaudrya Nyrania* Penn. Eu., *Edops* Penn.–L. Perm. NA. **F. Dendrerpetontidae,** *Branchiosauravus Dendrerpeton* [*Dendryazousa*] ?*Ichthyacanthus Platystegos* Penn. NA., *Eugyrinus Erpetocephalus* Penn. Eu. **F. Trimerorhachidae,** *Dendrysekos Pelion* Penn. NA., ?*Dawsonia* Penn. Eu., *Trimerorhachis* L. Perm. NA., ?*Lysipterygium* L. Perm. As. ?**F. Dvinosauridae,** ?*Chalcosaurus* M. Perm. Eu., *Dvinosaurus* U. Perm. Eu.

SUBORDER ERYOPSOIDEA. **F. Chenoprosopidae,** *Mytaras* Penn. NA., *Chenoprosopus* L. Perm. NA. **F. Archegosauridae,** *Archegosaurus* L. Perm. Eu., ?*Melosaurus Platyops* M. Perm. Eu. **F. Micropholidae,** *Micropholis* L. Trias. SAf. **F. Trematopsidae,** *Acheloma* ?*Parioxys Trematops* L. Perm. NA. **F. Zatrachyidae,** *Stegops* Penn. NA., *Platyrhinops* Penn. Eu., *Platyhystrix Zatrachys* L. Perm. NA., *Acanthostoma Dasyceps* L. Perm. Eu. **F. Eryopsidae,** ?*Lusor Mordax* ?*Potamochoston* Penn. Eu., "*Branchiosaurus*" Penn. NA., Penn.–L. Perm. Eu., *Onchiodon* Penn.–L. Perm. Eu., *Actinodon* [*Euchirosaurus*] *Chelydosaurus Leptorophus Micromelerpeton Osteophorus Protriton Sclerocephalus* [*Weissia*] L. Perm. Eu., *Eryops* [*Eryopsoides*] L. Perm. NA. **F. Dissorhophidae,** *Platyrhinops* Penn. NA., *Alegeinosaurus Aspidosaurus Broiliellus Cacops Dissorophus* ?*Tersomius* L. Perm. NA., *Zygosaurus* M. Perm. Eu.

SUBORDER NEORHACHITOMI. **F. Rhinesuchidae,** *Rhinesuchoides* M. Perm. SAf., *Rhinesuchus* M.–U. Perm. SAf., U. Perm. EAf., *Laccosaurus* U. Perm. SAf., *Laccocephalus Uranocentrodon* L. Trias. SAf. Mad., *Gondwanosaurus* L. Trias. SAs. **F. Lydekkerinidae,** *Lydekkerina Putterillia* L. Trias. SAf. **F. Benthosuchidae,** *Benthosuchus Thoösuchus Volgasuchus* L. Trias. Eu., *Wetlugosaurus* L. Trias. Eu. ?SAf., ?*Tungussogyrinus* L. Trias. NAs.

ORDER STEREOSPONDYLI. **F. Capitosauridae,** *Heptasaurus* L. Trias. Eu., *Parotosaurus* L. Trias. Eu. SAf., *Capitosaurus* L.–U. Trias. Eu., *Kestrosaurus* L. Trias. SAf., *Stanocephalosaurus* M. Trias. NA., *Mastodonsaurus* M.–U. Trias. Eu., *Cyclotosaurus* M.–U. Trias. Eu., U. Trias. Aus., ?*Austropelor* ?L. Jur. Aus. **F. Trematosauridae,** *Gonioglyptus* L. Trias. SAs., *Trematosuchus Rhytidosteus* [*Microposaurus*] L. Trias. SAf., *Trematosaurus* L. Trias. Eu. ?SAf., *Peltostega Platystega Tertrema* L. Trias. Spitz., *Lyrocephalus* L. Trias. Spitz. Gr., *Aphaneramma* [*Lonchorhynchus*] *Stoschiosaurus* L. Trias. Gr. **F. Metoposauridae,** *Anaschisma Borborophagus Buettneria Dictyocephalus Eupelor Kalamoiketor Koskinonodon* U. Trias. NA., *Metoposaurus* U. Trias. Eu. **F. Brachyopidae,** *Batrachosuchus* L.

Trias. SAf., *Bothriceps* M. Trias. Aus., *Brachyops ?Pachygonia* M. Trias. SAs., *Plagiosternum* M.–U. Trias. Eu., *Gerrhosaurus Gerrhothorax Plagiosaurus Plagiosuchus* U. Trias. Eu.

ORDER EMBOLOMERI. F. **Eogyrinidae,** *?Atopotera Calligenetheon Cricotus Eobaphetes Spondylerpeton* Penn. NA., *Eogyrinus Ichthyerpeton Pholiderpeton Pteroplax ?Memonomenos* Penn. Eu., *Archeria* L. Perm. NA. **F. Anthracosauridae,** *?Crassigyrinus* Miss. Eu., *Anthracosaurus* Penn. Eu. **F. Palaeogyrinidae,** *Palaeogyrinus* Penn. Eu. **F. Pholidogasteridae** *?Papposaurus* Miss. Eu., *Pholidogaster* Miss. Eu. ?NA. **Embolomeri?, Incertae sedis,** *Arkanserpeton Eosaurus* Penn. NA., *Nummulosaurus* L. Perm. Eu.

ORDER SEYMOURIAMORPHA. **F. Diplovertebrontidae,** *Diplovertebron Gephyrostegus* Penn. Eu., *Melanerpeton* Penn.–L. Perm. Eu., *Sparagmites* L. Perm. Eu., *Discosauriscus* [*Discosaurus*] L.–M. Perm. Eu. **F. Seymouridae,** *Conodectes Seymouria* L. Perm. NA., *?Lanthanosuchus* M. Perm. Eu. **F. Kotlassiidae,** *Kotlassia* U. Perm. Eu.

SUPERORDER SALIENTIA

ORDER EOANURA. **F. Amphibamidae,** *Amphibamus Miobatrachus* Penn. NA.

ORDER PROANURA. **F. Protobatrachidae,** *Protobatrachus* L. Trias. Mad.

ORDER ANURA

SUBORDER AMPHICOELA. **?F. Montsechobatrachidae,** *Montsechobatrachus* U. Jur. Eu., *?Eobatrachus* U. Jur. NA., *?Stremmia* U. Jur. Af. **F. Liopelmidae,** R. NA. NZ.

SUBORDER OPISTHOCOELA. **F. Discoglossidae,** R. Eu. As. NAf., *Latonia Pelophilus* Mioc. Eu., *Alytes* Mioc.–R. Eu., *Bombina* [*Bombinator*] Mioc.–R. Eu., R. EAs. **F. Pipidae,** R. Af. SA., *?Eoxenopoides* ?L. Tert. SAf., *Xenopus* Mioc.–R. Af.

SUBORDER ANOMOCOELA. **F. Pelobatidae,** R. NA. EAs. EInd. Seychelle Is., *Macropelobates* Olig. EAs., *Pelobates* Mioc.–R. Eu., *Eopelobates* Mioc. Eu., *Scaphiopus* Plioc.–R. NA. **F. Pelodytidae** R. Eu., *Propelodytes* Eoc. Eu., *Miopelodytes* Mioc. NA.

SUBORDER PROCOELA. **F. Palaeobatrachidae,** *Palaeobatrachus ?Protopelobates* Mioc. Eu. **F. Bufonidae,** R. Cos., *Indobatrachus* Eoc. As., *Bufo* Olig.–R. Eu., Plioc.–R. NA., Pleist.–R. As., R. Af. SA., *?Bufavus* Mioc. Eu., *Teracophrys* Mioc. SA., *?Diplopelturus ?Pliobatrachus* Plioc. Eu., *?Platosphus* Pleist. Eu., *Ceratophrys* Pleist.–R. SA. **F. Brachycephalidae,** R. SA. CA. WInd. **F. Hylidae,** R. NA. SA. Eu. As. Aus. NAf., *Hyla* [*Lithobatrachus*] Mioc.–R. Eu., R. NA. SA. As. Aus. NAf., *Amphignathodon* Olig.–Mioc. Eu., R. SA.

SUBORDER DIPLASIOCOELA. **F. Ranidae,** R. Cos., *Ranavus Aspherion* Mioc. Eu., *Rana* Mioc.–R. As. Eu., Plioc.–R. NA., R. Af. Aus. SA. **F. Polypedatidae,** R. Af. SAs. EInd. **F. Brevicipitidae,** R. NA. SA. Af. SAs. Aus.

SUBCLASS LEPOSPONDYLI

ORDER AISTOPODA. **F. Ophiderpetontidae,** *Ophiderpeton* ?Miss., Penn. Eu. Penn. NA. **F. Dolichosomidae,** *Dolichosoma* Penn. Eu., *Thyrsidium* Penn. NA.

ORDER NECTRIDIA. **F. Lepterpetontidae,** *Lepterpeton* Penn. Eu., *?Sauravus* L. Perm. Eu. **F. Urocordylidae,** *Urocordylus* [*Ctenerpeton Oestocephalus Ptyonius Sauropleura*] Penn. Eu. NA., *Crossotelos* L. Perm. NA. **F. Keraterpetontidae,** *Diceratosaurus* Penn. NA., *Batrachiderpeton Keraterpeton ?Scincosaurus* Penn. Eu., *Diplocaulus* L. Perm. NA.

ORDER MICROSAURIA (MICRAMPHIBIA, ADELOSPONDYLI). **F. Dolichopareiidae,** *Dolichopareias* Miss. Eu. **F. Adelogyrinidae,** *Adelogyrinus* Miss. Eu. **F. Lysorophidae,** *Coccytinus Molgophis Phlegethontia Pleuroptyx* Penn. NA., *Lysorophus* L. Perm. NA. **F. Microbrachidae,** *Hyloplesion Microbrachis* Penn. Eu. **F. Gymnarthridae,** *Cardiocephalus Eyryodus Gymnarthrus Pariotichus* L. Perm. NA., ?*Petrobates* L. Perm. Eu. **F. Pantylidae,** *Sparodus* ?*Ricnodon* Penn. Eu., *Pantylus* L. Perm. NA. **F. Ostodolepidae** ?*Orthocosta* ?*Seelya* Penn. Eu., *Ostodolepis* L. Perm. NA. ?**F. Phrynosuchidae** *Phrynosuchus* U. Perm. SAf. **Microsauria, incertae sedis:** *Asaphestera, Fritschia, Hylerpeton, Hylonomus, Leiocephalikon* Penn. NA.

ORDER URODELA

SUBORDER CRYPTOBRANCHOIDEA. **F. Hynobiidae,** R. EAs., ?*Wolterstorffiella* Mioc. Eu. **F. Cryptobranchidae,** R. NA. EAs., *Andrias* Mioc. Eu., *Plicognathus* Plioc. NA., *Megalobatrachus* Mioc. Eu., R. EAs.

SUBORDER AMBLYSTOMOIDEA. **F. Amblystomatidae,** R. NA., ?*Scapherpeton, Hemitrypus* U. Cret. NA., *Lanebatrachus Ogallalabatrachus Plioamblystoma* Plioc. NA., *Amblystoma* [*Ambystoma*] Pleist.–R. NA.

SUBORDER SALAMANDROIDEA. **F. Salamandridae,** R. Eu. As. NA., *Tylototriton* Eoc.–Mioc. Eu., R. EAs., *Heteroclitotriton Megalotriton* Eoc.–Olig. Eu., *Oligosemia* Olig. Eu., *Heliarchon Chelotriton Archaeotriton Palaeopleurodeles Polysemia* Mioc. Eu., *Salamandra* Mioc.–R. Eu., *Triturus* Mioc.–R. Eu., R. NA. **F. Amphiumidae** R. NA., *Amphiuma* ?Eoc. Eu., R. NA., *Batrachosauroides* Mioc. NA. **F. Plethodontidae** R. NA. SA. Eu.

SUBORDER PROTEIDA. **F. Proteidae,** R. Eu. NA., ?*Hylaeobatrachus* L. Cret. Eu., *Palaeoproteus* Eoc. Eu., *Orthophyia* Mioc. Eu.

SUBORDER MEANTES. **F. Sirenidae,** R. NA., *Siren* Pleist.–R. NA.

ORDER APODA (GYMNOPHIONA). **F. Coeciliidae,** R. SA. CA. Af. SAs. EInd.

CLASS REPTILIA

SUBCLASS ANAPSIDA

ORDER COTYLOSAURIA

SUBORDER CAPTORHINOMORPHA. **F. Solenodonsauridae,** ?*Eusauropleura* ?*Tuditanus* [*Eosauravus*] Penn. NA., *Solenodonsaurus* Penn. Eu. **F. Limnoscelidae,** *Limnoscelis* L. Perm. NA. **F. Captorhinidae,** *Captorhinus* [*Ectocynodon*] *Labidosaurus* ?*Pleuristion* L. Perm. NA. **F. Protorothyrididae,** *Protorothyris* ?*Puercosaurus Romeria* L. Perm. NA. ?**F. Millerettidae** *Milleretta* [*Millerina*] *Millerinoides* M. Perm. SAf.

SUBORDER DIADECTOMORPHA. **F. Diadectidae,** *Desmatodon* Penn. NA., *Animasaurus Bolbodon Chilonyx Diadectes Diasparactus Diadectoides Helodectes* L. Perm. NA., *Phanerosaurus Stephanospondylus* ?*Sphenosaurus* [*Parasaurus*] L. Perm. Eu. **F. Pareiasauridae,** *Brachypareia Bradysaurus Bradysuchus Dolichopareia Embrithosaurus Koalemasaurus Nochelesaurus Platyoropha* M. Perm. SA., *Parabradysaurus* M. Perm. Eu., *Propappus* M.–U. Perm. SAf., *Elginia Scutosaurus* [*Proelginia*] U. Perm. Eu., *Anthodon* U. Perm. Eu. EAf. SAf., *Pareiasuchus* U. Perm. Eu. SAf., *Nanopareia Pareiasaurus* U. Perm. SAf., ?*Sclerosaurus* L. Trias. Eu. **F. Bolosauridae,** *Bolosaurus* L. Perm. NA. **F. Procolophonidae,** *Nycteroleter Nyctiphruretus Rhipaeosaurus* M. Perm. Eu., *Owenetta* U. Perm. SAf., *Anomoiodon Koiloskiosaurus* L. Trias. Eu., *Microthelodon* [*Thelegnathus*] *Myocephalus Procolophon Spondylestes* L. Trias. SAf., *Telerpeton* M. Trias. Eu., *Hypsognathus* U. Trias. NA.

ORDER CHELONIA [TESTUDINATA]

SUBORDER EUNOTOSAURIA. **F. Eunotosauridae,** *Eunotosaurus* M. Perm. SAf.

SUBORDER AMPHICHELYDIA. **F. Triassochelidae,** *Proganochelys Triassochelys* U. Trias.

Eu. **F. Proterochersidae,** *?Chelyzoön* M.-U. Trias. Eu., *Chelytherium Proterochersis ?Saurodesmus* U. Trias. Eu. **F. Pleurosternidae,** *Platychelys* L.-U. Jur. Eu., *?Protochelys* M. Jur. Eu., *Stegochelys* U. Jur. Eu., *Pleurosternum* U. Jur.-L. Cret. Eu., *Glyptops* U. Jur.-U. Cret. NA., U. Jur. Eu., *Platycheloides* L. Cret. EAf., *Helochelydra* [*Peltochelys, Tretosternum*] L. Cret. Eu., *Helochelys Rhinochelys Trachydermochelys* U. Cret. Eu., *Neurankylus* U. Cret. NA. **F. Baënidae,** *Craspedochelys* U. Jur. Eu., *Naomichelys Probaëna* U. Jur. NA., *Boremys Charitemys Eubaëna ?Polythorax Thescelus* U. Cret. NA., *Baëna* U. Cret., Eoc. NA., *Chisternon* Eoc. NA. **F. Kallokibotidae,** *Kallokibotium* U. Cret. Eu. **F. Meiolanidae,** *Niolamia* U. Cret. SA., *Crossochelys* Eoc. SA., *Meiolania* Pleist. Aus. **F. Plesiochelidae,** *Hydropelta Parachelys Plesiochelys Tholemys* U. Jur. Eu., *Hylaeochelys* U. Jur.-L. Cret. Eu., *Brodiechelys* L. Cret. Eu., *?Scutemys* L. Cret. EAs.

SUBORDER PLEURODIRA. **F. Pelomedusidae,** R. SA. Af., *Amblypeza Bothremys* U. Cret. NA., *Naiadochelys* U. Cret. NA. SA., *Elochelys* U. Cret. Eu., *Podocnemis* U. Cret. NA., U. Cret.-Mioc. Eu., U. Cret.-R. SA., Paleoc.-Pleist. Af., Eoc. SAs., R. Mad., *Bantuchelys* Paleoc. Af., *Stereogenys* Eoc. NAf., *Taphrosphys* Eoc.-Mioc. NA., *Pelomedusa* Olig.-R. Af., *Sternothaerus* Mioc.-R. Af., *?Paralichelys* Plioc. Eu., *Shweboemys* Plioc. SAs. **F. Chelidae,** R. SA. SAs. Aus., *Chitracephalus* L. Cret. Eu., *Aperotemporalis* U. Cret. NAf., *?Polysternum* U. Cret.-Eoc. Eu., *Rhinemys* Eoc. As., R. SA., *Hydraspis* [*Acrohydraspis*] ?Eoc. SAs., Plioc.-R. SA., *Chelys* Tert.-R. SA., *Chelodina Emydura* Pleist.-R. Aus.

SUBORDER CRYPTODIRA. **F. Thalassemydidae,** *Chelonides Eurysternum* [*Achelonia Acichelys Aplax Euryespis Palaeomedusa*] *Idiochelys Thalassemys* U. Jur. Eu., *Pelobatochelys Tropidemys* U. Jur.-L. Cret. Eu., *Desmemys* L. Cret. Eu., *?Pygmaeochelys ?Sontiochelys* U. Cret. Eu., *Lytoloma* [*Erquelinnesia Euclastes Pachyrhynchus Puppigerus*] U. Cret. Eu. Af. NA., *Catapleura Desmatochelys* [*Atlantochelys Neptunochelys*] *Osteopygis Phyllemys* U. Cret. NA. SA. **F. Dermatemydidae,** R. CA., *Sinochelys* L. Cret. As., *Agomphus Homorophus Zygoramma* U. Cret. NA., *Compsemys* U. Cret.-Paleoc. NA., *Basilemys* U. Cret.-Eoc. NA., *Adocus* U. Cret.-Eoc. NA., Eoc. EAs., *Lindholmemys* U. Cret. As., *Hoplochelys* Paleoc.-Eoc. NA., *Alamosemys Anosteira Baptemys Kallistira Notomorpha Pseudanosteira* Eoc. NA., *Trachyaspis* Eoc.-Mioc. Eu. Af., *Xenochelys* Olig. NA. **F. Kinosternidae,** R. NA. SA., *Kinosternon* Plioc.-R. NA., R. SA. **F. Platysternidae,** R. EAs., *Sartemys* L. Cret. EAs. **F. Emydidae,** R. Eu. As. NAf. NA. SA., *Sinemys* L. Cret. EAs., *?Gyremys* U. Cret. NA., *Echmatemys* Eoc. NA., *Patanemys* Eoc. Eu., *Geoemyda* Eoc. Eu., Eoc.-R. As., R. CA. SA., *Ptychogaster* Eoc.-Mioc. Eu., *Chrysemys* [*Platemys*] Eoc.-Mioc. Eu., Pleist.-R. NA., R. SA., *Clemmys* [*Sharemys*] Eoc.-R. Eu. As., Mioc.-R. NA., R. NAf., *Ocadia* Eoc.-Mioc. Eu., Plioc. NAf., Plioc.-R. As., *Broilia* Olig. Eu., *Palaeochelys* Olig. Eu. As., *Cinixys* Olig. Eu., R. Af., *Emys* Paleoc.-R. Eu., R. NA. NAf. As., *Graptemys Trachemys* Olig.-R. NA., *Stylemys* ?Olig. As., Olig.-Plioc. NA., *Terrapene* [*Cistudo*] Mioc.-R. NA., *Clemmydopsis* Plioc. Eu., *Polyechmatemys* Plioc. EAs., *Hardella Kachuga Malayemys* [*Damonia*] Plioc.-R. As., *Deirochelys* Plioc.-R. NA., *Pseudemys* Plioc.-R. NA., R. SA., *Geoclemmys* Pleist.-R. EAs. **F. Testudinidae,** R. Eu. As. Af. NA. SA., *Achilemys Hadrianus* Eoc. NA., *Cheirogaster* Eoc. Eu., *Sinohadrianus* Eoc. EAs., *Homopus* Eoc.-R. Eu., R. Af., *Testudo* [*Colossochelys*] Eoc.-R. EAs. Af. NA. SA., *Cymatholcus* Olig. NA., *Bystra Bysmachelys* Plioc. NA., *Gopherus* Pleist.-R. NA. **F. Chelydridae,** R. NA. SA., *Gafsachelys* Eoc. Eu. NAf., *Chelydra* Olig.-Mioc. Eu., Pleist.-R. NA., R. SA., *Acherontemys* Mioc. NA., *Macroclemys*

[*Macrochelys*] Pleist.–R. NA. F. **Protostegidae,** *Archelon Protostega* U. Cret. NA., *Protosphargis* U. Cret. Eu., *Pseudosphargis* Olig. Eu. F. **Toxochelidae,** ?*Cynocercus Porthochelys Toxochelys* U. Cret. NA. F. **Chelonidae,** R. Oc., *Cratochelone* L. Cret. Aus., *Notochelone* Cret. Aus., *Allopleuron Glyptochelone Proeretmochelys* U. Cret. Eu., *Caretta* [*Thalassochelys*] U. Cret.–Eoc. Eu., Eoc. NAf., R. Oc., *Peritresius* U. Cret.–Mioc. NA., *Lembonax* Eoc. NA., *Argillochelys Eochelone Eosphargis* Eoc. Eu., *Chelonia* [*Chelone*] Eoc. Eu., Mioc.–Plioc. NA., R. Oc., *Chelydopsis Oligochelone* Olig. Eu., *Procolpochelys Syllomus* Mioc. NA. F. **Dermochelidae,** R. Oc., *Cosmochelys* Eoc. Af., *Psephophorus* Eoc. NAf., Eoc.–Mioc. NA., Eoc.–Plioc. Eu., *Dermochelys* Mioc. Eu., R. Oc. F. **Trionychidae,** R. As. Af. EInd. NA., *Plastomenus* U. Cret.–Eoc. NA., *Platypeltis* U. Cret.–R. NA., *Aspideretes* Cret.–Eoc. NA., Plioc.–R. SAs., *Conchochelys* Paleoc.–Eoc. NA., *Temnotrionyx* Eoc. NA., *Axestemmys* Eoc. NA., Mioc. Eu., *Trionyx* [*Amyda Aspidonectes Aulacochelys Castresia*] Eoc.–Plioc. Eu., Eoc.–R. NA., Olig.–R. As., Pleist.–R. EInd., *Cyclanorbis Cycloderma* Mioc.–R. Af., *Chitra* Plioc.–R. SAs., Pleist.–R. EInd; *Lissemys* [*Emyda*] Plioc.–R. SAs., F. **Carettochelidae,** R. New Guinea, *Akrochelys Alloechelys* Eoc. Eu., *Hemichelys* ?Eoc. SAs., *Anosteira* [*Pseudotrionyx*] Paleoc.–Olig. Eu., Eoc. NA. As., *Carettochelys* Mioc.–R. New Guinea.

SUBCLASS ICHTHYOPTERYGIA

ORDER ICHTHYOSAURIA. F. **Mixosauridae,** ?*Grippia* M. Trias. Spitz., *Mixosaurus* M. Trias. Eu. Spitz., Trias. EInd., ?Trias. NA., *Phalarodon* M. Trias. NA. F. **Shastasauridae,** *Cymbospondylus* M. Trias. NA. Eu., Trias. EInd., ?*Ekbainacanthus Pessosaurus* M. Trias. Spitz., *Pachygonosaurus* M. Trias. Eu., *Shastasaurus* M. Trias. Eu., U. Trias. NA., *Californosaurus* [*Delphinosaurus*] ?M. Trias. Eu., U. Trias. NA., *Merriamia Toretocnemus* U. Trias. NA. F. **Omphalosauridae,** *Omphalosaurus* M. Trias. NA., *Pessopteryx* M. Trias. Spitz. F. **Stenopterygiidae,** *Leptopterygius* ?U. Trias., L. Jur. Eu., ?U. Jur. SA., *Eurhinosaurus* L. Jur. Eu., *Stenopterygius* L.–M. Jur. Eu., Jur. SA., *Nannopterygius* U. Jur. Eu., *Platypterygius* L. Cret. Eu., *Cetarthrosaurus* U. Cret. Eu. F. **Ichthyosauridae,** *Ichthyosaurus* [*Eurypterygius*] L. Jur. Gr., L.–U. Jur. Eu., Jur. NA., *Macropterygius* L.–U. Jur. Eu., U. Jur. SA., *Ophthalmosaurus* [*Baptanodon*] L.–U. Jur. Eu., M. Jur.–U. Cret. NA., *Apatodonosaurus* U. Jur. NA., *Brachypterygius* U. Jur. Eu., *Myobradypterygius* U. Jur.–L. Cret. SA., *Myopterygius* L. Cret. Aus., L.–U. Cret. Eu., U. Cret. NA. SA. EInd. NZ.

SUBCLASS SYNAPTOSAURIA

ORDER PROTOROSAURIA. F. **Araeoscelidae,** *Araeoscelis Ophiodeirus* L. Perm. NA., *Kadaliosaurus* L. Perm. Eu., ?*Broomia* M. Perm. SAf., ?*Aphelosaurus* U. Perm. Eu. F. **Protorosauridae,** ?*Adelosaurus Protorosaurus* U. Perm. Eu., *Eifelosaurus* ?*Microcnemus* ?*Trachelosaurus* L. Trias. Eu. F. **Tanystropheidae,** *Macroscelosaurus Macrocnemus Tanystropheus* [*Tribelesodon*] *Zanclodon* M. Trias. Eu. F. **Trilophosauridae,** *Trilophosaurus* U. Trias. NA. F. **Weigeltisauridae** *Weigeltisaurus* [*Palaeochamaeleo*] U. Perm. Eu., *Coelurosauravus* U. Perm. Mad.

ORDER SAUROPTERYGIA

SUBORDER NOTHOSAURIA. F. **Nothosauridae,** *Ceresiosaurus Cymatosaurus Doliovertebra Germanosaurus Lamprosaurus Lariosaurus Macromirosaurus Microleptosaurus Opeosaurus Paranthosaurus Partanosaurus Proneusticosaurus Rhaeticonia* M. Trias. Eu., *Simosaurus* M.–U. Trias. Eu., *Nothosaurus* L.–U. Trias. Eu., ?Trias.

WAs., *Corosaurus* U. Trias. NA. **F. Pachypleurosauridae,** *Anarosaurus Dactylosaurus Neusticosaurus Pachypleurosaurus Phygosaurus Psilotrachelosaurus* M. Trias. Eu.

SUBORDER PLESIOSAURIA

INFRAORDER PISTOSAUROIDEA. **F. Pistosauridae,** *Pistosaurus* M. Trias. Eu.

INFRAORDER PLIOSAUROIDEA (BRACHYDEIRA). **F. Pliosauridae,** *Eurycleidus Thaumatosaurus* [*Rhomaleosaurus*] L. Jur. Eu., *Pliosaurus* L.–U. Jur. Eu., *Pantosaurus Peloneustes Simolestes* U. Jur. Eu. Af., *Kronosaurus* L. Cret. Aus. **F. Polycotylidae** *Brachauchenius Brimosaurus Piratosaurus Polycotylus Trinacromerum* U. Cret. NA., *Polyptychodon* U. Cret. Eu.

INFRAORDER PLESIOSAUROIDEA (DOLICHODEIRA). **F. Plesiosauridae,** *Eretmosaurus Macroplata Microcleidus Plesiosaurus Seeleyosaurus Sthenarosaurus* L. Jur. Eu., *Muraenosaurus Picrocleidus Tremamesacleis Tricleidus* U. Jur. Eu., *Cryptocleidus* [*Apractocleidus*] U. Jur. Eu. Gr., *Leptocleidus* L. Cret. Eu. **F. Elasmosauridae,** *Colymbosaurus* L. Jur. Eu., *Brancasaurus* L. Cret. Eu., *Alzadasaurus Aphrosaurus Cimoliosaurus Fresnosaurus Hydralmosaurus Hydrotherosaurus Leurospondylus Morenosaurus Ogmodirus Styxosaurus Thalassiosaurus Thalassomedon Thalassonomosaurus* U. Cret. NA., *Elasmosaurus* U. Cret. NA. Eu. Aus. NZ., *Mauisaurus* U. Cret. Aus. NZ.

SUBORDER PLACODONTIA. **F. Placodontidae,** *Placodus* L.–U. Trias. Eu., *Paraplacodus* M. Trias. Eu. **F. Cyamodontidae** *Cyamodus Saurosphargis* M. Trias. Eu., *Chelyoposuchus Henodus Placochelys Psephoderma Psephosaurus* U. Trias. Eu.

SUBCLASS LEPIDOSAURIA

ORDER EOSUCHIA

SUBORDER YOUNGINIFORMES. **F. Younginidae,** *Galesphyrus Heleophilus ?Heleosaurus ?Heleosuchus ?Noteosuchus Paliguana Palaeagama Saurosternon Youngina Youngoides Youngopsis* U. Perm. SAf. **F. Prolacertidae,** *Prolacerta* L. Trias. SAf. **F. Tangasauridae,** *Hovasaurus* U. Perm. Mad., *Tangasaurus* L. Trias. E. Af. Mad.

SUBORDER CHORISTODERA. **F. Champsosauridae,** *Champsosaurus* U. Cret.–Eoc. Eu. NA., ?Cret. EInd., ?Eoc. Af., *Simoedosaurus* U. Cret.–Eoc. Eu.

?SUBORDER THALATTOSAURIA. **F. Thalattosauridae,** *Nectosaurus Thalattosaurus* U. Trias. NA.

SUBORDER ACROSAURIA. **F. Pleurosauridae,** *Pleurosaurus* [*Acrosaurus*] U. Jur. Eu.

ORDER RHYNCHOCEPHALIA. **F. Sphenodontidae** R. NZ., *Palacrodon* L. Trias. SAf., *Brachyrhinodon Clevosaurus ?Pachystropheus Polysphenodon* U. Trias. Eu., *Homoeosaurus Meyerasaurus* U. Jur. Eu., *Ophisthias Theretairus* U. Jur. NA., *Chometokadmon* L. Cret. Eu. **?F. Sapheosauridae,** *Sapheosaurus Sauranodon* U. Jur. Eu. **F. Claraziidae,** *Clarazia Hescheleria* M. Trias. Eu. **F. Rhynchosauridae,** *Howesia Mesosuchus* L. Trias. SAf., *Stenaulorhynchus* M. Trias. EAf., *Cephalonia Scaphonyx* M. Trias. SA., *Rhynchosaurus Stenometopon* U. Trias. Eu., *Hyperodapedon* U. Trias. Eu. SAs., *Paradapedon* U. Trias. SAs.

ORDER SQUAMATA

SUBORDER LACERTILIA [SAURIA]

INFRAORDER GEKKOTA. **F. Gekkonidae,** R. Cos. **F. Uroplatidae,** R. Mad.

INFRAORDER IGUANIA. **F. Iguanidae,** R. NA. SA. Mad., *Chamops* U. Cret. NA., *Iguanavus* U. Cret.–Eoc. NA., *Exostinus* Cret.–Olig. NA., *Parasauromalus* Eoc. NA., *Proiguana* Eoc. Eu., *Aciprion* Olig. NA., *Tetralophosaurus* Mioc. NA., *Crotaphytus* Plioc.–R. NA., *Leiosaurus* Plioc.–R. SA., *Phrynosoma* Pleist.–R. NA., *Iguana*

Pleist.–R. WInd., R. CA. SA. **F. Agamidae,** R. Eu. As. Af. Aus., *Conicodontosaurus Macrocephalosaurus* U. Cret. EAs., *Agama* Eoc.–R. Eu., R. As. Af., *Chlamydosaurus* Pleist.–R. Aus.

INFRAORDER RHIPTOGLOSSA. **F. Chamaeleontidae,** R. Af. Mad. SAs., ?*Mimosaurus* U. Cret. EAs., ?*Tinosaurus* Eoc. NA. EAs.

INFRAORDER SCINCOMORPHA. ?**F. Ardeosauridae,** *Ardeosaurus* U. Jur. Eu. **F. Xantusiidae,** R. NA. CA. WInd. **F. Scincidae,** R. Cos., *Cadurcosaurus* Eoc. Eu., *Protrachysaurus* Eoc.–Olig. Eu., *Dracaenosaurus* Olig. Eu., *Didosaurus* Pleist. Mauritius. **F. Dibamidae,** R. EInd. **F. Anelytropsidae,** R. NA. **F. Feyliniidae,** R. Af. **F. Lacertidae,** R. Eu. As. Af., *Lacerta* Eoc.–R. Eu., Pleist.–R. As., R. Af., *Nucras* Olig. Eu., R. Af. **F. Gerrhosauridae,** R. Af. **F. Teiidae,** R. NA. SA., *Tupinambis* Olig.–R. SA., *Cnemidophorus* Plioc.–R. NA., R. SA.

INFRAORDER AMPHISBAENIA. **F. Amphisbaenidae,** R. Eu. Af. NA. SA., *Lestophis* [*Limnophis Palaeoboa Ototriton*] Eoc. NA., *Hyporhina* Olig. NA., *Rhineura* Olig.–R. NA., *Crythiosaurus* Olig. EAs.

INFRAORDER ANGUIMORPHA. **F. Euposauridae,** *Euposaurus* U. Jur. Eu., ?*Monjurosaurus* L. Cret. EAs. **F. Zonuridae,** R. Af. **F. Pygopodidae,** R. Aus. **F. Helodermatidae,** R. NA. Borneo, *Heloderma* Olig.–R. NA. **F. Anguidae,** R. Eu. As. NAf. NA. SA., *Isodontosaurus* U. Cret. EAs., *Peltosaurus* U. Cret.–Olig. NA., *Placosaurus* Eoc. Eu., *Melanosaurus* Eoc. NA., *Xestops* Eoc.–Olig. NA., *Glyptosaurus* Eoc.–Olig. NA., Eoc. EAs., *Ophisaurus* [*Pseudopus*] Olig.–R. Eu., R. As. NAf. NA., *Propseudopus* Mioc. Eu., *Diploglossus* ?Mioc. Eu., R. CA. WInd. SA., *Anguis* Mioc.–R. Eu., R. NAf. WAs. **F. Xenosauridae,** R. CA. **F. Anniellidae,** R. NA.

INFRAORDER PLATYNOTA. **F. Varanidae,** R. Af. As. Aus., *Palaeosaniwa Parasaniwa Polyodontosaurus* U. Cret. NA., *Telmasaurus* U. Cret. EAs., *Provaranosaurus* Paleoc. NA., *Saniwa* [*Thinosaurus*] Paleoc.–Olig. NA. Eu., *Palaeovaranus Progonosaurus* Eoc. Eu., *Varanus* Eoc.–Plioc. Eu., Plioc.–R. As., Pleist.–R. Aus., *Megalania* Plioc. As., Pleist. Aus. **F. Dolichosauridae,** *Acteosaurus Adriosaurus Eidolosaurus Pontosaurus* L. Cret. Eu., *Dolichosaurus* U. Cret. Eu. **F. Aigialosauridae,** *Aigialosaurus Carsosaurus Mesoleptos Opetiosaurus* L. Cret. Eu. **F. Mosasauridae,** *Amphekepubis Ancylocentrum* [*Brachysaurus*] *Baptosaurus Clidastes Diplotomodon Elliptonodon Holcodus Holosaurus Kolposaurus Macrosaurus Nectoportheus Plesiotylosaurus Polygonodon Sironectes* U. Cret. NA., *Globidens* U. Cret. NA. Eu. NAf. EInd., *Platecarpus* U. Cret. NA. Eu. ?NAf., *Tylosaurus* [*Leiodon*] U. Cret. NA. Af., *Mosasaurus* U. Cret. NA. Af. Eu., *Leptosaurus* U. Cret. NAf., ?*Coniasaurus Dollosaurus Hainosaurus Plioplatecarpus Prognathosaurus* U. Cret. Eu., *Taniwhasaurus* U. Cret. NZ.

INCERTAE SEDIS: **F. Arretosauridae,** *Arretosaurus* Eoc. EAs. **F. Shinisauridae,** R. As. **F. Polyglyphanodontidae,** *Paraglyphanodon Polyglyphanodon* U. Cret. NA.

GENERA INCERTAE SEDIS: *Ceniogenys Macellodus* U. Jur. NA., *Saurillus* U. Jur. Eu., *Alethesaurus Habrosaurus Lanceosaurus Megasaurus Odaxosaurus Prionosaurus* U. Cret. NA., *Harpagosaurus* U. Cret.–Paleoc. NA., *Dicarlesia* [*Carlesia*] U. Cret. SA., *Haplodontosaurus Machaerosaurus Oligodontosaurus* Paleoc. NA., *Naocephalus Paraprionosaurus* Eoc. NA., *Enigmatosaurus* Eoc. Eu., *Crematosaurus Diacium* Olig. NA.

SUBORDER SERPENTES [OPHIDIA]. **F. Palaeophidae,** *Pachyophis* L. Cret. Eu., *Simoliophis* U. Cret. Eu. NAf. Mad., *Archaeophis* Eoc. Eu., *Palaeophis* [*Dinophis*] Eoc. Eu. NA. Af., *Pterosphenus* Eoc. NAf. NA. **F. Boidae,** R. NA. SA. As. Af., *Boavus Lestophis Lithophis Protagras* Eoc. NA., *Madtsoia* Eoc. SA., *Paleryx* Eoc. Eu., *Gigantophis* Eoc. NAf., *Palaeopython* Eoc.–Mioc. Eu., *Calamagras* [*Aphelophis*] Olig. NA., *Ogomophis* Olig.–Mioc. NA., *Bothropis Heteropython Scaptophis* Mioc. Eu. **F. Pythonidae,** *Daunophis* Plioc. As., *Python* Plioc.–R. As., Pleist.–R. Aus., R. Af. **F. Typhlopidae,** R. NA. SA. As. Af. Aus. **F. Aniliidae (Ilysiidae),** R. SA. As., *Dinilysia* U. Cret. SA., *Scytalophis* Olig. Eu. **F. Uropeltidae Xenopeltidae,** R. As. **F. Colubridae,** R. Cos., *Tachyophis* Olig. Eu., *Pylmophis* Olig.–Mioc. Eu., *Protropidonotus Sansanosaurus* Mioc. Eu., *Elaphe* [*Elaphis*] Mioc.–R. Eu., R. As. NA. CA., *Palaeoelaphe* Plioc. NA., *Farancia Pituophis Thamnophis* Pleist.–R. NA., *Drymarchon* Pleist.–R. NA., R. SA., *Coluber* [*Zamenis*] Pleist.–R. Eu. NA., R. As. CA., *Ptyas* Pleist.–R. As., *Natrix* [*Tropidonotus*] Pleist.–R. NA., R. Eu. As. Af. Aus. **F. Elapidae,** R. As. Af. Aus. NA. SA., *Palaeonaja* Mioc.–Plioc. Eu., *Naja* Pleist.–R. As. **F. Hydrophidae,** R. As. Aus. EInd. **F. Viperidae,** R. Eu. As. Af., ?*Coniophis* U. Cret. NA., ?*Helagras* Paleoc. NA., *Provipera* Mioc. Eu., *Vipera* Mioc.–R. Eu., R. As. Af., *Bitis* Plioc. Eu., R. Af. **F. Crotalidae,** R. NA. SA. As., *Crotalus* Pleist.–R. NA.

SUBCLASS ARCHOSAURIA

ORDER THECODONTIA

SUBORDER PSEUDOSUCHIA. **F. Erythrosuchidae,** *Erythrosuchus Proterosuchus* L. Trias. SAf., *Chasmatosaurus* L. Trias. SAf. As., *Chasmatosuchus* L. Trias. Eu. **F. Ornithosuchidae,** *Browniella Euparkeria* L. Trias. SAf., ?*Dongusia* L. Trias. Eu., ?*Parringtonia* M. Trias. EAf., *Erpetosuchus Ornithosuchus Saltoposuchus* U. Trias. Eu., *Scleromochlus* Trias. Eu. **F. Aëtosauridae,** *Aëtosaurus Dyoplax* U. Trias. Eu. **F. Sphenosuchidae,** *Sphenosuchus* U. Trias. SAf. **F. Stagonolepidae,** *Stagonosuchus* M. Trias. EAf., *Hoplitosuchus Prestosuchus Procerosuchus Rauisuchus Rhadinosuchus* M. Trias. SA., *Episcoposaurus* [*Desmatosuchus*] *Stegomus Stegomosuchus* U. Trias. NA., *Stagonolepis* U. Trias. Eu., ?*Platyognathus* U. Trias. EAs. *Typothorax* U. Trias. NA. ?SAs.

SUBORDER PHYTOSAURIA (PARASUCHIA). **F. Phytosauridae,** *Mesorhinus* L. Trias. Eu., *Angistorhinopsis Ebrachosaurus Ebrachosuchus Frankosuchus Mystriosuchus Phytosaurus* [*Belodon*] *Termatosaurus* U. Trias. Eu., *Angistorhinus Clepsysaurus Leptosuchus Machaeroprosopus Palaeorhinus Promystriosuchus Rutiodon* U. Trias. NA., *Brachysuchus* U. Trias. NA. SAs.

ORDER CROCODILIA (LORICATA)

SUBORDER PROTOSUCHIA. **F. Notochampsidae,** *Protosuchus* U. Trias. NA., *Erythrochampsa Notochampsa* ?*Pedeticosaurus* U. Trias. SAf.

SUBORDER SEBECOSUCHIA. **F. Sebecidae,** *Sebecus* Eoc. SA.

SUBORDER MESOSUCHIA. **F. Teleosauridae,** *Aeolodon Mystriosaurus Pelagosaurus* L. Jur. Eu., *Teleidosaurus* M. Jur. Eu., *Anglosuchus Teleosaurus* M.–U. Jur. Eu., *Steneosaurus* M.–U. Jur. Eu., Jur. Mad. SA., *Mycterosuchus* U. Jur. Eu., ?*Heterosaurus* L. Cret. Eu. **F. Metriorhynchidae (Thalattosuchia),** *Metriorhynchus* [*Suchodus*] M.–U. Jur. Eu., Jur. SA., *Circosaurus Dacosaurus* U. Jur. Eu., *Geosaurus* [*Neustosaurus*] U. Jur.–L. Cret. Eu., *Enaliosuchus* L. Cret. Eu. **F. Pholidosauridae,** *Crocodilaemus Petrosuchus* U. Jur. Eu., *Pholidosaurus* U. Jur.–L. Cret. Eu., *Suchosaurus* L. Cret. Eu. **F. Dyrosauridae,** *Teleorhinus* U. Cret. NA., *Dyrosaurus* U. Cret.–Eoc. Af., *Congosaurus* ?Paleoc. Af., *Rhabdognathus Sokotosaurus Wurnosaurus* Eoc. Af. **F. Atoposauridae,** ?*Hoplosuchus* U. Jur. NA., *Alligatorellus Alligatorium Atoposaurus* U. Jur. Eu. **F. Notosuchidae,** ?*Brasileosaurus Cynodontosuchus Notosuchus Uruguaysuchus* U. Cret. SA., *Libycosuchus* U. Cret. NAf. **F. Goniopholidae,** *Amphicotylus* U. Jur. NA., *Nannosuchus Oweniasuchus Therio-*

suchus U. Jur. Eu., *Goniopholis* [*Hyposaurus*] U. Jur.–L. Cret. Eu., U. Jur. ?U. Cret. NA., L.–U. Cret. SA., *Machimosaurus* U. Jur. ?L. Cret. Eu., *Bernissartia* L. Cret. Eu., *Shamosuchus* L. Cret. EAs., *Coelosuchus ?Pinacosuchus ?Pliogonodon ?Polydectes* U. Cret. NA., *Microsuchus Symptosuchus* U. Cret. SA., *Doratodon* U. Cret. Eu., *Baharijodon* U. Cret. NAf.

SUBORDER EUSUCHIA. **F. Hylaeochampsidae,** *Hylaeochampsa* ?U. Jur. L. Cret. Eu., *?Heterosuchus* L. Cret. Eu. **F. Stomatosuchidae,** *Stomatosuchus ?Stromerosuchus* U. Cret. NAf., *Dollosuchus* Eoc. Eu. **F. Aegyptosuchidae,** *Aegyptosuchus* U. Cret. NAf. **F. Crocodylidae,** R. As. Af. NA. SA. Aus., *Thoracosaurus* U. Cret. NA. SA. Eu., *Holops* U. Cret. NA., ?U. Cret. SA., *Phobosuchus* [*Deinosuchus*] U. Cret. Eu. NA., *Allodaposuchus* U. Cret. Eu., *Necrosuchus* ?U. Cret. ?Paleoc. SA., *Leidyosuchus* U. Cret.–Paleoc. NA., ?U. Cret. SA., *Crocodylus* [*Crocodilus Thecachampsa*] U. Cret.–Mioc. Eu., Eoc.–R. Af. NA., Mioc.–R. SA., Plioc.–R. As., Pleist.–R. Aus. EInd., *Navajosuchus* Paleoc. NA., *Asiatosuchus* Eoc. As., *Brachyuranochampsa Orthogenysuchus* Eoc. NA., *Eosuchus Pristichampsus Weigeltisuchus* Eoc. Eu., *Arambourgia* Eoc.–Olig. Eu., *Tomistoma* Eoc.–Plioc. Af., Mioc. Eu., R. As., *Gavialosuchus* Mioc. Eu., Plioc. NA., *Euthecodon* Plioc. NAf., *Gryposuchus Leptorrhamphus Rhamphostomopsis* Plioc. SA., *Emysuchus* ?Pleist. SA., *Pallimnarchus* Pleist. Aus. **F. Alligatoridae,** R. NA. SA. As., *Dinosuchus* L. Cret. SA., *Brachychampsa Prodiplocynodon* U. Cret. NA., *Bottosaurus* U. Cret. NA., ?U. Cret. SA., *Notocaiman* Paleoc. SA., *Ceratosuchus* Paleoc. NA., *Allognathosuchus* Paleoc.–Olig. NA., *Boverisuchus Caimanosuchus Eocenosuchus Hassiacosuchus Menatalligator* Eoc. Eu., *Diplocynodon* Eoc.–Mioc. Eu., *Eocaiman* Eoc. SA., *Hispanochampsa* Olig. Eu., *Alligator* [*Caimanoidea*] Olig.–R. NA., R. As., *Brachygnathosuchus Proalligator* Plioc. SA., *Paleosuchus* [*Jacaretinga*] Plioc.–R. SA., *Caiman* [*Purussaurus Xenosuchus*] Plioc.–R. SA., R. CA. **F. Gavialidae,** R. As., *Gavialis* [*Leptorhynchus Rhamphostoma*] Eoc. Eu., Plioc.–R. As., ?Plioc. Af., Pleist.–R. EInd., *Rhamphosuchus* Plioc. As.

ORDER PTEROSAURIA

SUBORDER RHAMPHORHYNCHOIDEA. **F. Dimorphodontidae,** *Campylognathus Dimorphodon Dorygnathus Parapsicephalus* L. Jur. Eu., *Rhamphocephalus* M. Jur. Eu., *Anurognathus Scaphognathus* U. Jur. Eu. **F. Rhamphorhynchidae,** *?Doratorhynchus Odontorhynchus* U. Jur. Eu., *Rhamphorhynchus* U. Jur. Eu., ?EAf., *?Dermodactylus* U. Jur. NA.

SUBORDER PTERODACTYLOIDEA. **F. Pterodactylidae,** *Ctenochasma Gnathosaurus Belonochasma* U. Jur. Eu., *Pterodactylus* [*Ornithocephalus*] U. Jur.–L. Cret. Eu., U. Jur. EAf. **F. Ornithocheiridae,** *Ornithocheirus* [*Cretornis*] ?U. Jur., L.–U. Cret. Eu., *Ornithodesmus* L. Cret. Eu., *Criorhynchus Lonchodectes* L.–U. Cret. Eu. **F. Pteranodontidae,** *Ornithostoma* L. Cret. Eu., *Nyctosaurus* [*Nyctodactylus*] U. Cret. NA., *Pteranodon* U. Cret. NA. Eu.

ORDER SAURISCHIA

SUBORDER THEROPODA

INFRAORDER COELUROSAURIA. **F. Ammosauridae,** *Ammosaurus* U. Trias. NA. **F. Procompsognathidae** *Procompsognathus Pterospondylus* U. Trias. Eu. **F. Podokesauridae,** *Avipes ?Dolichosuchus Halticosaurus Saltopus Velocipes* U. Trias. Eu., *Coelophysis Podokesaurus* U. Trias. NA., *?Lukousaurus* U. Trias. EAs. **F. Segisauridae,** *?Hallopus Segisaurus* Jur. NA. **F. Coeluridae,** *Sarcosaurus* L. Jur. Eu., *Iliosuchus* M. Jur. Eu., *Agrosaurus* Jur. Aus. *Sinocoelurus* Jur. EAs., *Caudocoelus* U. Jur. Eu., *Ornitholestes* U. Jur. NA., *Elaphrosaurus* U. Jur. EAf., ?U. Cret. NAf., *Coelurus* U. Jur. ?L. Cret. NA., *Aristosuchus Calamospondylus Thecocoelurus ?Thecospondylus* L. Cret. Eu., *Dryptosaurus* L. Cret. NA., *Coeluroides Dryptosauroides Jubbulpuria Laevisuchus* U. Cret. SAs., *?Fulgurotherium* U. Cret. Aus. **F. Compsognathidae,** *Compsognathus* U. Jur. Eu., *?Saurornithoides* L. Cret. EAs., *Velociraptor* U. Cret. EAs., *Compsosuchus* U. Cret. SAs., *Rapator* U. Cret. Aus., *?Brasileosaurus* U. Cret. SA., *Dromaeosaurus* U. Cret. NA. **F. Ornithomimidea,** *Chirostenotes Macrophalangia ?Stenonychosaurus Struthiomimus* U. Cret. NA. *Ornithomimus* U. Cret. NA. EAs., *Clasmodosaurus Loncosaurus* U. Cret. SA., *Betasuchus* U. Cret. Eu., *Oviraptor* U. Cret. EAs., *Ornithomimoides* U. Cret. SAs., *Walgettosuchus* U. Cret. Aus.

INFRAORDER CARNOSAURIA. **F. Palaeosauridae,** *Palaeosaurus* U. Trias. Eu. **F. Gryponychidae,** *Aetonyx Gryponyx* U. Trias. SAf. **F. Teratosauridae,** *Cladyodon Gresslyosaurus Pachysaurus Teratosaurus* [*Zanclodon*] U. Trias. Eu., *?Basutodon ?Orinosaurus* U. Trias. SAf., *Sinosaurus* U. Trias. EAs., *Zatomus* U. Trias. NA. **F. Ceratosauridae,** *Proceratosaurus* M. Jur. Eu., *Ceratosaurus* U. Jur. NA. ?EAf., *?Labrosaurus* U. Jur. NA. ?Eu. ?EAf. *Chienkosaurus* U. Jur. EAs. **F. Megalosauridae,** *Sarcosaurus* L. Jur. Eu., *Megalosaurus* [*Aggiosaurus Altispinax Magnosaurus Poikilopleuron Streptospondylus*] L. Jur.-L. Cret. Eu., U. Jur. EAf., *Iliosuchus Nuthetes* U. Jur. Eu., *?Szechuanosaurus* U. Jur. EAs. *Embasaurus* L. Cret. WAs. **F. Allosauridae** *Creosaurus Saurophagus* U. Jur. NA., *Allosaurus* U. Jur. NA. ?EAf., *Antrodemus* L. Cret. NA. EAs., *Carcharodontosaurus* U. Cret. NAf., *Indosaurus Indosuchus Orthogoniosaurus* U. Cret. SAs. **F. Spinosauridae,** *Bahariasaurus Spinosaurus* U. Cret. NAf., *Erectopus* U. Cret. Eu. NAf. **F. Deinodontidae** *Aublysodon Deinodon Genyodectes Dromaeosaurus Gorgosaurus Tyrannosaurus* U. Cret. NA., *Albertosaurus* U. Cret. NA. ?EAs., *Alectrosaurus ?Prodeinodon* U. Cret. EAs.

INFRAORDER PROSAUROPODA. **F. Thecodontosauridae** *Spondylosoma* M. Trias. SA., *Yaleosaurus* ["*Anchisaurus*"] U. Trias. NA. *Thecodontosaurus* U. Trias. Eu. NA. SAf. ?EAf. *Dromicosaurus* U. Trias. SAF. *Gyposaurus* U. Trias. SAf. EAs. *Massospondylus* U. Trias. SAf. EAf. SAs. **F. Plateosauridae,** *Plateosaurus* U. Trias. Eu. *Lufengosaurus Yunnanosaurus* U. Trias. EAs. **F. Plateosauravidae,** *Euskelosaurus Gigantoscelus Plateosauravus* U. Trias. SAf. **F. Melanorosauridae,** *Eucnemesaurus Melanorosaurus* U. Trias SAf.

SUBORDER SAUROPODA. **F. Cetiosauridae,** *Rhaetosaurus* L. Jur. Aus., *Cetiosaurus* [*Cetiosauriscus*] M. Jur.-L. Cret. Eu., *Amphicoelias Barosaurus Diplodocus Elosaurus Haplocanthosaurus* U. Jur. NA., *Dicraeosaurus Tornieria* [*Gigantosaurus*] U. Jur. EAf., *Aepisaurus* L. Cret. Eu., *Macrurosaurus* L.-U. Cret. Eu., *Titanosaurus* L. Cret. Eu., U. Cret. SAs. SA., *Mongolosaurus* L. Cret. EAs., *Hypselosaurus Magyarosaurus Succinodon* U. Cret. Eu., *Aegyptosaurus* U. Cret. NAf., *Alamosaurus* U. Cret. NA., *Argyrosaurus Campylodon* U. Cret. SA., *Antarctosaurus* U. Cret. SA. SAs., *Laplatasaurus* U. Cret. SA. SAs. Mad. **F. Brachiosauridae,** *Bothriospondylus* M.-U. Jur. Eu., Jur. Mad., *Apatosaurus* [*Brontosaurus*] *Dystrophaeus Uintasaurus* U. Jur. NA., *Brachiosaurus* U. Jur. NA. EAf., *Camarasaurus* [*Morosaurus*] U. Jur. NA., L. Cret. Eu., *Pleurocoelus* [*Astrodon*] L.-U. Cret. NA., L. Cret. Eu., *? Algoasaurus* L. Cret. SAf., *Austrosaurus* L. Cret. Aus., *Pelorosaurus* L. Cret. Eu., *Helopus Tienshanosaurus* L. Cret. EAs., *Asiatosaurus Omeisaurus* U. Cret. EAs. "*Neosaurus*" U. Cret. NA.

ORDER ORNITHISCHIA

SUBORDER ORNITHOPODA. **F. Hypsilophodontidae,** *?Geranosaurus* U. Trias. SAf., *Dysalotosaurus* U. Jur. EAf., *Hypsilophodon* L. Cret. Eu., *Parksosaurus* U. Cret. NA., *Thescelosaurus* U. Cret. NA. **F. Iguanodontidae,** *Cryptodraco* M. Jur. Eu., ?*Nanosaurus* U. Jur. NA., *Laosaurus* [*Dryosaurus*] U. Jur. NA., *Camptosaurus* U. Jur.–L. Cret. NA., *Anoplosaurus* ?*Eucercosaurus Iguanodon* ?*Priodontognathus Vectisaurus* L. Cret. Eu., *Craspedodon Rhabdodon* [*Mochlodon*] U. Cret. Eu., *Kangnasaurus* Cret. Af. **F. Hadrosauridae (Trachodontidae),** *Anatosaurus Cheneosaurus Claosaurus Corythosaurus Edmontosaurus Hadrosaurus Hypacrosaurus Kritosaurus* [*Gryposaurus*] *Lambeosaurus Parasaurolophus Procheneosaurus* [*Tetragonosaurus*] *Prosaurolophus Thespesius* U. Cret. NA., *Saurolophus* U. Cret. NA. As., *Trachodon* U. Cret. NA. Eu., *Orthomerus Syngonosaurus* U. Cret. Eu., *Bactrosaurus Jaxartosaurus Mandschurosaurus Nipponosaurus Tanius* U. Cret. EAs. **F. Psittacosauridae,** *Protiguanodon Psittacosaurus* L. Cret. EAs., ?*Stenopelix* L. Cret. Eu. **F. Troödontidae,** *Pachycephalosaurus Troödon* U. Cret. NA.

SUBORDER STEGOSAURIA. **F. Scelidosauridae,** *Scelidosaurus* L. Jur. Eu. **F. Stegosauridae,** *Sarcolestes* M. Jur. Eu., *Omosaurus* M.–U. Jur. Eu., *Stegosaurus* ?M. Jur. Eu., U. Jur. NA., *Diracodon* U. Jur. NA., *Echinodon* U. Jur. Eu., *Kentrurosaurus* U. Jur. EAf., *Craterosaurus* L. Cret. Eu., *Priconodon* L. Cret. NA.

SUBORDER ANKYLOSAURIA. **F. Acanthopholidae,** *Hylaeosaurus* [*Regnosaurus*] L. Cret. Eu., *Acanthopholis* L.–U. Cret. Eu., *Rhodanosaurus Struthiosaurus*, U. Cret. Eu. **F. Nodosauridae,** *Hoplitosaurus* L. Cret. NA., *Polacanthus Polacanthoides* L. Cret. Eu., *Ankylosaurus Edmontonia Dyoplosaurus Euoplocephalus Hierosaurus Nodosaurus Palaeoscincus Panoplosaurus Scolosaurus Stegopelta* U. Cret. NA., *Anodontosaurus Loricosaurus* U. Cret. SA., ?*Brachypodosaurus Lametasaurus* U. Cret. SAs., *Pinacosaurus* U. Cret. EAs.

SUBORDER CERATOPSIA. **F. Protoceratopsidae,** *Protoceratops* U. Cret. EAs., *Leptoceratops* U. Cret. NA. **F. Ceratopsidae,** *Anchiceratops Arrhinoceratops Brachyceratops Chasmosaurus Ceratops Eoceratops Monoclonius Styracosaurus Torosaurus Triceratops* U. Cret. NA., *Pentaceratops* U. Cret. NA. As., ?*Notoceratops* U. Cret. SA.

SUBCLASS SYNAPSIDA

ORDER PELYCOSAURIA

SUBORDER OPHIACODONTIA. **F. Ophiacodontidae,** *Clepsydrops* Penn. NA., *Ophiacodon* [*Poliosaurus Theropleura*] *Varanosaurus* L. Perm. NA. **?F. Mesenosauridae,** *Mesenosaurus* M. Perm. Eu. **F. Eothyrididae,** *Baldwinonus Bayloria Eothryis Stereophallodon* ?*Tetraceratops* L. Perm. NA.

SUBORDER SPHENACODONTIA. **F. Varanopsidae,** ?*Aerosaurus* ?*Scoliomus Varanops* L. Perm. NA., ?*Anningia* ?*Elliotsmithia* M. Perm. SAf. **F. Sphenacodontidae,** *Macromerion* Penn. Eu. *Bathygnathus Ctenospondylus Dimetrodon Sphenacodon* L. Perm. NA., *Haptodus* [*Palaeohatteria Pantelosaurus*] *Neosaurus Oxyodon* L. Perm. Eu., ?*Phthinosaurus* M. Perm. Eu. ?*Ctenosaurus* L. Trias. Eu.

SUBORDER EDAPHOSAURIA. **F. Edaphosauridae,** *Edaphosaurus* [*Naosaurus*] Penn.–L. Perm. Eu. NA. **F. Lupeosauridae,** *Lupeosaurus* L. Perm. NA. **F. Nitosauridae,** *Mycterosaurus* [*Eumatthevia*] *Nitosaurus* L. Perm. NA. **F. Caseidae** *Casea Cotylorhynchus* L. Perm. NA. **?F. Galeopsidae (Dromasauria),** *Galeops Galepus* M. Perm. SAf., *Galechirus* U. Perm. SAf. **Edaphosauria incertae sedis:** *Glaucosaurus*, *Trichasaurus* L. Perm. NA.

INCERTAE SEDIS: SUBORDER OR ORDER MESOSAURIA. **F. Mesosauridae,** *Mesosaurus* L. Perm. SA. SAf., *Stereosternum* L. Perm. SA., *Noteosaurus* L. Perm. SAf.

ORDER THERAPSIDA

SUBORDER DINOCEPHALIA

INFRAORDER TITANOSUCHIA. F. **Rhopalodontidae,** *Brithopus* [*Orthopus Dinosaurus Eurosaurus*] *Cliorhizodon Rhopalodon Titanophoneus* M. Perm. Eu. F. **Titanosuchidae,** *Anteosaurus Broomisuchus* [*Dinosuchus*] *Dinartamus Dinocynodon Dinopolus Dinosphaegus ?Enobius Jonkeria* [*Dinophoneus Phoneosuchus*] *Scapanodon Scullya Titanognathus Titanosuchus* M. Perm. SAf.

INFRAORDER TAPINOCEPHALIA. F. **Deuterosauridae,** *Deuterosaurus* [*Mnemeiosaurus Uraniscosaurus*] M. Perm. Eu., *?Lamiasaurus* M. Perm. SAf. F. **Venjukoviidae,** *Venjukovia* [*Myctosuchus*] M. Perm. Eu. F. **Tapinocephalidae,** *Ulemosaurus* M. Perm. Eu., *? Archaeosuchus Ceratocephalus Criocephalus Delphinognathus ?Eccasaurus ?Lamiasaurus Mormosaurus Moschops Moschognathus Moschosaurus Pelosuchus Pnigalion Struthiocephalus Tapinocephalus* [*Phocosaurus*] *Taurocephalus Taurops* M. Perm. SAf.

SUBORDER DICYNODONTIA. F. **Dicynodontidae,** *Dicynodon* [*Dicranozygoma Eurycarpus Keirognathus Oudenodon*] M.-U. Perm. SAf. EAf. Eu., L. Trias. EAs., M. Trias. SA. *?Cerataelurus* M. Perm. SAf. *Aulacocephalodon* [*Bainia*] *Aulacocephalus Chelyrhynchus Dicynodontoides Diictodon Dinanomodon Eocyclops Eosimops Mastocephalus Myosauroides Orophicephalus Palemydops Pelanomodon Pelorocyclops Platycyclops Platypodosaurus Pylaecephalus Rhachicephalodon* U. Perm. SAf., *Cisticephalus Megacyclops Rhachiocephalus* U. Perm. SAf. EAf., *Haughtoniana* U. Perm. EAf., *Geikia Gordonia* U. Perm. Eu., *Kannemeyeria* [*Sagecephalus Ptychocynodon*] *Myosaurus* L. Trias. SAf., *Dinodontosaurus Stahleckeria* M. Trias. SA., *Sinokannemeyeria* M. Trias. EAs., *Placerias* U. Trias. NA. F. **Endothiodontidae,** *Brachyuraniscus ?Cerataelurus Chelyoposaurus Cryptocynodon Cteniosaurus Diaelurodon Emydochampsa Emydopsis Emydopsoides Emydorhinus Emydorhynchus Emyduranus Endogomphodon Esoterodon Eumantellia Eurychororhinus Newtonella Palemydops Pristerodon* [*Opisthoctenodon*] *Prodicynodon Synostocephalus Taognathus Tropidostoma* U. Perm. SAf., *Endothiodon Emydops* U. Perm. SAf. EAf., *Pachytegos* U. Perm. EAf. F. **Lystrosauridae,** *Lystrosaurus* [*Mochlorhinus Ptychognathus Ptychosiagum Prolystrosaurus Rhabdocephalus*] L. Trias. SAf. As. ?Eu.

SUBORDER THERIODONTIA

INFRAORDER GORGONOPSIA. F. **Gorgonopsidae,** *Broomisaurus* [*Scymnorhinus*] *Cyniscodon Eoarctops Eriphostoma Hipposaurus Pachyrhinos* M. Perm. SAf., *Scylacognathus* M.-U. Perm. SAf., *Galesuchus* M.-U. Perm. EAf., *Aelurosauroides Aloposaurus Cerdognathus Cerdorhinus Cynarioides Cynariops Cyniscops Cynodraco Delphaciognathus* [*Asthenognathus*] *Dinogorgon Galerhynchus Gorgonops Gorgonognathus Gorgonorhinus Ictidorhinus Leontocephalus Leptotrachelus Lycaenodontoides Lycaenops Prorubidgea Rubidgea Sycosaurus* U. Perm. SAf., *Chiwetasaurus Dixeya Tetraodon* U. Perm. EAf., *Aelurognathus Aelurosaurus Arctognathoides Arctops Galerhinus Lycaenodon Scymnognathus* U. Perm. EAf. SAf., *Lycaenoides Scylacops* U. Perm. SAf. ?EAf., *Arctognathus* U. Perm. SAf. Eu., *Inostrancevia* [*Amalitzkia*] U. Perm. Eu. F. **Burnetiidae** *?Styracocephalus* M. Perm. SAf., *Burnetia* U. Perm. SAf.

INFRAORDER CYNODONTIA. F. **Procynosuchidae,** *Paracynosuchus* U. Perm. SAf., *Procynosuchus* U. Perm. SAf. EAf. F. **Cynosauridae,** *Cynosaurus* [*Cynosuchus*] *Cynosuchoides* U. Perm. SAf. F. **Galesauridae,** *Dvinia* [*Permocynodon*] U. Perm. Eu., *Parathrinaxodon* U. Perm. EAf., *Micrictodon Nanictosuchus* U. Perm. SAf., *Galesaurus* [*Glochinodon*] *Glochinodontoides Nanictosaurus Notictosaurus Nythosaurus Platycraniellus Thrinaxodon* [*Ictidopsis*] L. Trias. SAf. **F. Cynognathidae,** *Bauríoides Cynidiognathus Cynognathus Cynogomphius Lycaenognathus Lycognathus* [*Lycochampsa*] ?*Tribolodon* L. Trias. SAf. **F. Chiniquodontidae,** *Belesodon Chiniquodon* M. Trias. SA. **F. Diademodontidae,** *Cyclogomphodon Cynochampsa Diademodon Gomphognathus Octogomphus Protacmon Trirachodon Trirachodontoides* L. Trias. SAf. **F. Traversodontidae,** *Gomphodontosuchus Traversodon* M. Trias. SA.

INFRAORDER THEROCEPHALIA. **F. Pristerognathidae,** *Alopecodon Alopecognathus Alopecorhinus Glanosuchus Hyaenosuchus Hyorhynchus* ?*Ictidoparia Lycedops Lycosaurus Lycosuchus Pristerognathus Scymnosaurus* ?*Theriodesmus Trochorhinus Trochosaurus Trochosuchus* M. Perm. SAf., *Cynariognathus* M.–U. Perm. SAf., ?*Arctosuchus Scylacoides* U. Perm. SAf. **F. Alopecopsidae,** *Alopecideops Pardosuchus Scylacosaurus* [*Scylacorhinus*] M. Perm. SAf., *Akidognathus Alopecopsis Cerdosuchoides Cerdosuchus Hofmeyeria Notaelurodon Notaelurops* U. Perm. SAf., *Anna* U. Perm. Eu. **F. Whaitsiidae,** *Hyenosaurus Moschorhynchus Tigrisuchus Whaitsia* U. Perm. SAf., *Moschorhinus Notosollasia Theriognathus* U. Perm. SAf. EAf., *Euchambersia* U. Perm. SAf. ?Eu. **F. Scaloposauridae** *Cerdodon Simorhinella* M. Perm. SAf. *Icticephalus Ictidosaurus* M–U. Perm. SAf. ?*Arnognathus Chaerosaurus Ictidodon Ictidognathus Ictidostoma Ictidosuchoides Ictidosuchops Lycideops* ?*Macroscelesaurus Nanicticephalus Nanictidops Octocynodon Pelictosuchus Scalopocephalus Scaloposaurus Scaloposuchus* U. Perm. SAf., *Ericiolacerta* L. Trias. SAf. **F. Bauriidae,** *Aelurosuchus Bauria Bauroides Melinodon Microgomphodon Microhelodon Sesamodon Watsoniella* L. Trias. SAf.

THERIODONTIA INCERTAE SEDIS: *Mygalesaurus Mygalesuchus Rubidgina* U. Perm. SAf.

ORDER ICTIDOSAURIA. **F. Dromatheriidae,** ?*Karroomys* L. Trias. SAf., ?*Lycorhinus* ?*Pachygenelus* U. Trias. SAf., *Dromatherium Microconodon* U. Trias. NA. **F. Trithelodontidae,** *Trithelodon* U. Trias. SAf. **F. Microcleptidae,** ?*Eozostrodon Hysiprymnopsis Microcleptes* [*Microlestes*] *Thomasia* ?*Tricuspes* ?*Uniserium* U. Trias. Eu. **F. Tritylodontidae,** *Bienotherium* U. Trias. EAs., *Tritylodon* U. Trias. SAf., *Chalepotherium Mucrotherium Triglyphus* U. Trias. Eu. *Oligokyphus* U. Trias.–L. Jur. Eu., *Stereognathus* M. Jur. Eu.

CLASS AVES

SUBCLASS ARCHAEORNITHES

ORDER ARCHAEOPTERYGIFORMES. **F. Archaeopterygidae,** *Archaeopteryx Archaeornis* U. Jur. Eu.

SUBCLASS NEORNITHES

SUPERORDER ODONTOGNATHAE

ORDER HESPERORNITHIFORMES. **F. Hesperornithidae,** *Hargeria Hesperornis* U. Cret. NA. **F. Enaliornithidae,** *Enaliornis* L. Cret. Eu., *Neogaeornis* U. Cret. Eu. **F. Baptornithidae,** *Baptornis* U. Cret. NA., ?*Eupterornis* Eoc. Eu.

ORDER ICHTHYORNITHIFORMES. **F. Ichthyornithidae,** *Ichthyornis* U. Cret. NA. **F. Apatornithidae** *Apatornis* ?*Cimolopteryx* U. Cret. NA.

SUPERORDER PALAEOGNATHAE

?ORDER CAENAGNATHIFORMES. **F. Caenagnathidae,** *Caenagnathus* U. Cret. NA.

ORDER STRUTHIONIFORMES. **F. Struthionidae,** R. Af. WAs., *Struthio* Plioc.–Pleist. Eu. As., Plioc.–R. Af., R. WAs.

ORDER RHEIFORMES. **F. Rheidae,** R. SA., *Heterorhea* Plioc. SA., *Rhea* Pleist.–R. SA.

ORDER CASUARIIFORMES. **F. Casuariidae,** R. Aus., *Casuarius* Pleist.–R. Aus. **F. Dromiceiidae,** R. Aus., *Dromiceius* Pleist.–R. Aus. **F. Dromornithidae,** *Dromornis Genyornis* Pleist. Aus.

ORDER DINORNITHIFORMES. **F. Dinornithidae,** *Dinornis* Pleist. NZ. **F. Anomalopterygidae,** *Megalapteryx Anomalopteryx Emeus Euryapteryx* Pleist. NZ.

ORDER AEPYORNITHIFORMES. **F. Aepyornithidae,** *?Psammornis* Eoc. Af., *Eremopezus Stromeria* Olig. NAf., *Aepyornis Mullerornis* Pleist. Mad.

ORDER APTERYGIFORMES. **F. Apterygidae,** R. NZ., *Metapteryx* Pleist. Aus., *Pseudapteryx* Pleist. NZ., *Apteryx* Pleist.–R. NZ.

ORDER TINAMIFORMES. **F. Tinamidae,** R. SA., *Tinamisornis* Plioc. SA., *Rhynchotus Nothura Crypturus Tinamus* Pleist.–R. SA.

SUPERORDER NEOGNATHAE

ORDER GAVIIFORMES. **F. Gaviidae (Colymbidae),** R. Eu. As. NA., *Colymboides* Eoc.–Olig. Eu., *Gaviella* Olig. NA., *Gavia* Pleist.–R. Eu. NA., R. As.

ORDER COLYMBIFORMES. **F. Colymbidae (Podicipedidae),** R. Cos., *Colymbus* Olig.–R. NA., Plioc.–R. Eu., Pleist. Mauritius, Pleist.–R. SA. As., R. Aus. Af., *Podilymbus Aechmophorus* Pleist.–R. NA., R. SA.

ORDER PROCELLARIIFORMES. **F. Diomedeidae,** R. Oc., *Diomedea* Plioc.–Pleist. Eu., Pleist. NZ. NA., R. Oc. **F. Procellariidae,** R. Oc., *Puffinus* Olig.–Pleist. Eu., Mioc.–Pleist. NA., Pleist. Aus. NZ., R. Oc., *Hydrornis Plotornis* Mioc. Eu., *Procellaria* Mioc. Eu., R. Oc., *Fulmarus* Pleist. NA. Eu., R. Oc., *Pterodroma* Pleist. SA., R. Oc. **F. Hydrobatidae,** R. Oc. **F. Pelecanoididae,** R. Oc. **Genus incertae sedis** *Gigantornis* Eoc. Af.

ORDER SPHENISCIFORMES. **F. Spheniscidae,** R. Ant. SAtl. SPac., *Palaeospheniscus* Olig.–Mioc. SA., *Paraspheniscus Perispheniscus Palaeoapteryodytes Argyrodyptes Pseudospheniscus Neculus Metancylornis Isotremornis Paraptenodytes Arthrodytes Treleudytes* Mioc. SA., *Delphinornis* Mioc. Seymour Is. SA., *Ichthyopteryx Eospheniscus Anthropornis Pachypteryx Orthopteryx* Mioc. Seymour Is., *Palaeeudyptes Pachydyptes* Mioc. NZ., *Eudyptes* Pleist. NZ., R. Ant. **F. Cladornithidae** *Cladornis Cruschedula* Olig. SA.

ORDER PELECANIFORMES

SUBORDER PHAËTHONTES. **F. Phaëthontidae,** R. Oc., *Prophaëton* Eoc. Eu., *Phaëthon* Pleist. Rodriguez, R. Oc.

SUBORDER PELECANI. **F. Pelecanidae,** R. Cos., *Protopelecanus* Eoc. Eu., *Pelecanus* Olig.–R. Eu., Plioc.–R. As., Pleist.–R. Aus. NA., R. SA. **F. Cyphornithidae,** *Cyphornis Palaeochenoides* Mioc. NA. **F. Pelagornithidae,** *Argillornis* Eoc. Eu., *Pelagornis* Mioc. Eu., *Liptornis* Mioc. SA. **F. Sulidae,** R. Oc., *Sula* Olig.–Pleist. Eu., Mioc. NA., Pleist. Rodriguez, R. Oc., *Miosula* Mioc., NA., *Morus* Mioc.–R. NA., R. Oc. **F. Elopterygidae,** *Elopteryx* U. Cret. Eu., *Actiornis Eostega* Eoc. Eu. **F. Phalacrocoracidae,** R. Cos., *?Graculavus* Eoc. NA., *Oligocorax* Olig. Eu. NA., *Phalacrocorax* Olig.–R. NA. Eu., Pleist.–R. Aus. SA., R. As. Af., *Miocorax* Mioc. Eu. NA., *Paracorax* Plioc. Eu. As., *Australocorax* Pleist. Aus. **F. Anhingidae,** R. As. Af. Aus. NA. SA., *Anhinga* Plioc. Eu., Pleist. Mauritius, Pleist.–R. Mad. Aus. NA., R. Af. As. SA.

SUBORDER FREGATAE. **F. Fregatidae,** R. Oc.

SUBORDER ODONTOPTERYGES. **F. Odontopterygidae,** *Odontopteryx* Eoc. Eu. **F. Pseudodontornithidae,** *Pseudodontornis* Horizon ? Loc. ?

ORDER CICONIIFORMES

SUBORDER ARDEAE. **F. Ardeidae,** R. Cos., *Botauroides Eocornis* Eoc. NA., *Proherodius* Eoc. Eu., *Goliathia* Olig. NAf., *Proardea* Olig.–Mioc. Eu., *Ardeacites Botaurites* Mioc. Eu., *Ardea* Mioc.–R. Eu., Pleist.–R. NA. SA., R. As. Aus. Af., *Mesophoyx* Pleist. Mad., R. Af. As. Aus., *Hydranassa Nyctanassa Leucophoyx Florida* Pleist.–R. NA., R. SA., *Butorides* Pleist.–R. Mauritius NA., R. SA. Af. As. Aus., *Nycticorax* Pleist.–R. Cos., *Casmerodius* Pleist.–R. NA. WInd., R. SA. Af. As. Eu. Aus., *Ardeola* Pleist.–R. Eu., R. As. Af. EInd., *Egretta* Pleist.–R. Eu., R. As. Af. Aus., *Botaurus* Pleist.–R. Eu. NA., R. As. Af. Aus. SA., *Ixobrychus* Pleist.–R. WInd. SA., R. Eu. As. Af. Aus. NA. Oc. **F. Cochleariidae,** R. CA. SA.

SUBORDER BALAENICIPITES. **F. Balaenicipitidae,** R. Af.

SUBORDER CICONIAE. **F. Scopidae,** R. Af. **F. Ciconiidae,** R. Cos., *Ibidopsis* Eoc. Eu., *Palaeophippiorhynchus* Olig. NAf., *Propelargus* Olig. Eu., *Pelargodes* Olig.–Mioc. Eu., *Ibidopodia* Mioc. Eu., *Protibis* Mioc. SA., *Ibis* Mioc. Eu., Pleist. Aus. SA., Pleist.–R. As., R. Af. EInd., *Amphipelargus* Plioc. WAs., *Ciconia* Plioc.–R. Eu., Plioc.–Pleist. NA., R. As. Af., *Leptoptilos* Plioc.–R. As., R. Af. EInd., *Palaeopelargus Xenorhynchopsis* Pleist. Aus., *Palaeociconia* Pleist. SA., *Jabiru* Pleist. WInd., R. CA. SA., *Xenorhynchus* Pleist.–R. Aus., R. SAs. EInd., *Euxenura* Pleist.–R. SA., *Mycteria* Pleist.–R. NA., R. SA. **F. Threskiornithidae,** R. Cos., *Guara Ajaia* Pleist.–R. NA., R. SA. *Platalea* Pleist.–R. Aus. Mad., R. Eu. As. Af., *Plegadis* Pleist.–R. NA., R. SA. Eu. As. Af. Aus.

SUBORDER PHOENICOPTERI. **F. Agnopteridae,** *Agnopterus* Eoc. Eu. **F. Scaniornithidae,** *Scaniornis Parascaniornis* U. Cret. Eu. **F. Phoenicopteridae,** R. Eu. As. Af. NA. SA., *Elornis* Eoc.–Olig. Eu., *Phoenicopterus* Olig.–R. Eu., Plioc.–R. NA., Pleist.–R. SA. NA. Mauritius, R. As. Af. *Palaelodus* Mioc. Eu.

ORDER ANSERIFORMES

SUBORDER ANHIMAE. **F. Anhimidae,** R. SA.

SUBORDER ANSERES. **F. Paranyrocidae,** *Paranyroca* Mioc. NA. **F. Anatidae,** *?Gallornis* U. Cret. Eu., *Romainvillia* Eoc. Eu., *Eonessa* Eoc. NA., *Loxornis* Olig. SA., *?Chenornis Cygnopterus* Olig. Eu., *Anser* Mioc.–R. Eu., Plioc.–R. As., Pleist.–R. NA., *Anas* Olig.–R. Eu., Mioc.–R. Af., Plioc.–R. NA., Pleist.–R. As. Aus. NA., Subrecent Mauritius, R. SA., *Presbychen* Mioc. NA., *Eoneornis Eutelornis* Mioc. SA., *Cygnavus* Mioc. Eu., *Nyroca* Mioc.–R. Eu., Pleist.–R. Aus. NZ., R. As. Af. SA., *Cygnus* Mioc.–R. Eu., Pleist.–R. NA., R. As. Af. SA., *Spatula* Plioc. Eu., Pleist.–R. NA., R. Cos., *Anabernicula* Plioc.–Pleist. NA., *Dendrocygna* Plioc.–R. NA., Pleist.–R. WInd. Aus., R. SA. Af. As. EInd. Oc., *Mergus* Plioc.–R. As. Eu., Pleist.–R. NA., R. SA., *Chen* Plioc.–R. NA., *Branta* Plioc.–R. NA., R. Eu. As., *Cygnopsis* Plioc.–R. As., *Euryanas Cnemiornis* Pleist. NZ., *Chendytes* Pleist. NA., *Centrornis* Pleist. Mad., *Archeoquerquedula* Pleist. SA., *Archaeocycnus* Pleist. Aus., *Nettapus* Pleist. Aus., R. Af., *Chenopis* Pleist. NZ., R. Aus., *Chenalopex* Pleist. SA. Mad., R. Af.. *Sarkidiornis* Pleist. Mauritius, R. As. Af. SA., *Aix Lophodytes* Pleist.–R NA., *Clangula* Pleist.–R. NA., R. Eu. As., *Biziura* Pleist.–R. Aus., *Somateria* Pleist.–R. Eu., R. As. NA., *Polysticta Histrionicus* Pleist.–R. NA., R. As., *Tadorna* Pleist.–R. As., R. Eu. As. Af., *Melanitta Oidemia* Pleist.–R. NA., R. Eu. As., *Chaulelasmus* Pleist.–R. NA., R. Eu. As. NAf., *Mareca* Pleist.–R. NA., R. SA. Eu. As. NAf.

ORDER FALCONIFORMES

SUBORDER CATHARTAE. **F. Cathartidae,** R. NA. SA., *Eocathartes* Eoc. Eu., *Phasmagyps Palaeogyps* Olig. NA., *Plesiocathartes* Olig. Eu., *Sarcorhamphus* Plioc.–R. NA., Pleist.–R. SA., *Breagyps* Pleist. NA., *Gymnogyps* Pleist.–R. NA., *Vultur* Pleist. NA., R. SA., *Cathartes* Pleist.–R. NA. SA., *Coragyps* Pleist.–R. NA., R. SA. F. **Teratornithidae** ?*Tapinopus* Eoc. Eu., *Teratornis Cathartornis* Pleist. NA.

SUBORDER FALCONES. F. **Sagittariidae,** R. Af., *Amphiserpentarius* Olig.–Mioc. Eu. F. **Accipitridae,** R. Cos., *Palaeocircus* ?*Lithornis* Eoc. Eu., ?*Teracus* Olig. Eu., *Palaeoplancus* Olig. NA., *Aquilavus* Olig.–Mioc. Eu., *Buteo* Olig.–R. NA., Mioc.–R. Eu., Pleist.–R. As., R. SA. Af., *Aquila* Olig.–R. Eu., Plioc.–R. Af., Pleist.–R. As. NA., *Palaeohierax Palaetus* Mioc. Eu., *Miohierax* Mioc. NA., *Proictinia Palaeoborus* Mioc.–Plioc. NA., *Haliaeetus* Mioc.–R. Eu., Pleist.–R. NA., R. As. Af., *Hypomorphnus* Mioc.–R. NA., R. SA., *Milvus* Mioc.–R. Eu., Pleist.–R. As., R. Af. Aus., *Neophrontops* Plioc.–Pleist. NA., *Parabuteo* Plioc.–R. NA., R. SA., *Accipiter* Plioc.–R. Eu., Pleist. Mauritius Mad., Pleist.–R. WInd. Aus. NA., R. As. Af. SA. Oc., *Neogyps Wetmoregyps* Pleist. NA., *Harpagornis* Pleist. NZ., *Asturaetus Taphaetus* ?*Palaeolestes Necrastur* Pleist. Aus., *Morphnus* Pleist. NA., R. CA. SA., *Spizaëtus* Pleist. WInd., Pleist.–R. NA., R. SA. As. EInd., *Elanus* Pleist.–R. NA., R. SA. Aus. As. Af., *Neophron Gypaëtus* Pleist.–R. As., R. Eu. Af., *Gyps* Pleist.–R. Eu., R. Af. As. *Uroaëtus* Pleist.–R. Aus., *Aviceda* Pleist.–R. Aus., R. Af. As., *Circus* Pleist.–R. NZ. NA., R. Eu. As. Af. Aus. SA. F. **Pandionidae,** R. Cos., *Pandion* Pleist.–R. NA., R. Cos. F. **Falconidae,** R. Cos., *Thegornis* ?*Badiostes* Mioc. SA., *Falco* Mioc.–R. NA., Plioc.–R. Eu. As., Pleist.–R. NZ. WInd., R. SA. Af. Aus., *Sushkinia* Plioc. WAs., *Foetopterus* Plioc.–Pleist. SA., *Lagopterus* Pleist. SA., *Colohierax Titanohierax* Pleist. NA., *Polyborus* Pleist.–R. WInd. NA., R. SA.

ORDER GALLIFORMES

SUBORDER GALLI. F. **Megapodiidae,** R. EInd. Aus., *Chosornis* Pleist. Aus. F. **Gallinuloididae,** *Gallinuloides* Eoc. NA. F. **Cracidae,** R. NA. SA., *Ortalis* Mioc.–R. NA., R. SA. F. **Tetraonidae,** R. Eu. As. NA., *Palaeophasianus* Eoc. NA., *Palaeoalectoris* Mioc. NA., *Palaeotetrix Dendragapus* Pleist. NA., *Tympanuchus Pedioecetes Bonasa Centrocercus* Pleist.–R. NA., *Lagopus* Pleist.–R. Eu., R. As. NA. F. **Phasianidae,** R. Cos., *Paraortix Palaeortyx* Eoc.–Mioc. Eu., ?*Filholornis* Olig. Eu., *Archaeophasianus* Olig.–Mioc. NA., *Palaeocryptonyx* Olig.–Plioc. Eu., *Palaeoperdix Miogallus Pliogallus Taoperdix* Mioc. Eu., ? *Anissolornis* Mioc. SA., *Miophasianus* Mioc. NA., *Cyrtonyx* Mioc.–R. NA., *Francolinus* Plioc. Eu., Pleist.–R. As., R. Af., *Gallus* Plioc. Eu., ?Pleist. NZ., Pleist.–R. As., R. EInd., *Alectoris* Plioc. Eu., R. As. NAf., *Phasianus* Plioc.–Pleist. Eu., Plioc.–R. As., *Colinus* Plioc.–R. NA., R. CA. WInd., *Tetrao* Plioc - R. Eu., R. As., *Perdix* Plioc.–R. Eu., Pleist.–R. As., *Dendrortyx Lophortyx Oreortyx* Pleist.–R. NA., *Chrysolophus Crossoptilon Pucrasia Tragopan Syrmaticus* Pleist.–R. As., *Coturnix* Pleist.–R. As., R. Eu. Af. Aus. F. **Numididae,** R. Af. F. **Meleagridae** R. NA., *Meleagris* Olig.–R. NA., *Parapavo* Plioc.–Pleist. NA.

SUBORDER OPISTHOCOMI. F. **Opisthocomidae,** R. SA.

ORDER GRUIFORMES

SUBORDER MESOENATIDES. F. **Mesoenatidae,** R. Mad.

SUBORDER TURNICES. F. **Turnicidae,** R. Af. As. Aus., *Turnix* Pleist.–R. As., R. Eu. Af. Aus. F. **Pedionomidae,** R. Aus.

SUBORDER GRUES. F. **Geranoididae,** *Geranoides* Eoc. NA. F. **Eogruidae,** *Eogrus* Eoc. As. F. **Gruidae,** R. Eu. As. Af. Aus. NA., *Aletornis Paragrus Fulicaletornis* Eoc. NA., *Geranopsis* Eoc. Eu., *Palaeogrus* Eoc.–Mioc. Eu., *Probalaerica* Mioc. Eu., *Urmiornis* Plioc. WAs. Eu., *Pliogrus* Plioc. Eu., *Grus* Plioc.–R. NA., Pleist.–R. Eu.

As., R. WInd. F. **Aramidae**, R. NA. SA., ?*Laornis* Eoc. NA., *Aramiellus Badistornis* Olig. NA., *Aramornis* Mioc. NA., *Euryonotus* Plioc. SA., *Aramus* Pleist.–R. NA., R. SA. F. **Psophiidae**, R. SA. F. **Orthocnemidae**, *Orthocnemus Elaphrocnemus* Olig. Eu. F. **Rallidae**, R. Cos., *Eocrex Palaeorallus* ?*Telmatornis* Eoc. NA., *Telecrex* Eoc. EAs., *Gypsornis* Eoc. Eu., *Quercyrallus* Eoc.–Olig. Eu., *Palaeocrex* Olig. NA., *Rallus* Eoc.–R., Eu. Pleist. NZ., Pleist.–R. NA., R. SA. Af. As. Aus., *Palaeoaramides Paraortygometra Rallicrex Pararallus Miorallus Miofulica* Mioc. Eu., *Thiornis* Plioc. Eu., *Creccoides* Plioc. NA., *Gallinula* Plioc.–R. NA., Pleist.–R. Aus. WInd., R. SA. As. Af. Oc., *Aptornis Diaphorapteryx Nesolimnas Palaeolimnas Cabalus* Pleist. NZ., *Nesotrochis* Pleist. WInd., *Microtribonyx* Pleist. Aus., *Epirallus* Pleist. NA., *Aramides* Pleist. NA., R. CA. SA., *Tribonyx* Pleist. Mad., Pleist.–R. Aus., *Ocydromus Notornis Gallirallus* Pleist.–R. NZ., *Porzana* Pleist.–R. WInd., R. Eu. As. Af. Aus. SA. WInd. Oc., *Fulica* Pleist.–R. NA. Mauritius Aus. NZ., R. Eu. SA. As. Af., *Porphyrio* Pleist.–R. Aus., R. Eu. Af. As., *Aphanapteryx* Subrecent Mauritius Rodriguez.

SUBORDER HELIORNITHES. F. **Heliornithidae**, R. Af. SAs. SA.

SUBORDER RHYNOCHETI. F. **Rhynochetidae**, R. Oc.

SUBORDER EURYPYGAE. F. **Eurypygidae**, R. CA. SA.

SUBORDER PHORORHACI. F. **Phororhacidae**, *Andrewsornis* Olig. SA., *Phororhacos* Olig.–Mioc. SA., *Callornis Psilopterus Pelecyornis* Mioc. SA., *Prophororhacus* Plioc. SA. F. **Brontornithidae**, *Physornis* Olig. SA., *Brontornis Rostrornis Liornis Moreno-Merceratia Lophiornis Ameghinia Staphylornis Palaeociconia* Mioc. SA. F. **Opisthodactylidae**, *Opisthodactylus* Mioc. SA.

SUBORDER CARIAMAE. F. **Bathornithidae**, *Bathornis* Olig. NA. F. **Hermosiornithidae**, *Hermosiornis Procariama* Plioc. SA. F. **Cariamidae**, R. SA.

SUBORDER OTIDES. F. **Otidae** R. Eu. As. Af., *Palaeotis* Mioc. Eu., *Otis* Mioc.–R. Eu.

ORDER DIATRYMIFORMES. F. **Diatrymidae**, *Diatryma* Eoc. NA. ?Eu., *Barornis Omorhamphus* Eoc. NA., *Eleutherornis* Eoc. Eu. F. **Gastornithidae**, *Gastornis Remiornis* Eoc. Eu.

ORDER CHARADRIIFORMES

SUBORDER CHARADRII. F. **Jacanidae**, R. Af. SAs. Aus. CA. SA., *Jacana* Pleist.–R. SA. F. **Rostratulidae**, R. Af. SAs. EInd. Aus. SA., *Rhynchaeites* Eoc. Eu. F. **Haematopodidae**, R. Cos., *Paractiornis* Mioc. NA., *Haematopus* Pleist.–R. Eu. NZ., R. NA. SA. Af. As. Oc. F. **Charadriidae**, R. Cos., *Dolichopterus* Olig. Eu., ?*Limicolavis* ?Olig. NA., *Vanellus* Olig.–R. Eu., Pleist. SA., R. As., *Charadrius* [*Aegialitis*] Mioc.–R. NA., Pleist.–R. Eu., R. As. Af. Aus. SA. Oc., *Himantopus* Mioc.–R. Eu., Pleist.–R. NZ., R. As. Af. NA. SA., *Eupoda* Pleist.–R. NA., R. As. Af. Aus., *Oxyechus* Pleist.–R. NA., R. SA. Af., *Lobivanellus* Pleist.–R. Aus., R. EInd. Af. As., *Squatarola* Pleist.–R. Eu., R. Af. As. NA. SA., *Eudromias* Pleist.–R. Eu., R. As. NAf. F. **Scolopacidae**, R. Cos., *Palaeotringa* ?*Graculavus* Eoc. NA., *Numenius* Eoc.–R. Eu., Pleist.–R. NA., R. Af. As. Aus. SA., *Totanus* Eoc.–R. Eu., Pleist.–R. NA. SA., R. As. Af. Aus., *Philohela* ?Eoc., R. NA., *Elorius* Mioc. Eu. *Scolopax* Mioc.–R. Eu., Pleist. NA., R. As. EInd., *Limosa* Mioc.–R. NA., R. Af. As. SA. Eu. Aus. Oc., *Tringa* Mioc.–R. Eu., R. As. Af. Aus., *Micropalama* Plioc.–R. NA., R. SA., *Coenocorypha* Pleist.–R. NZ., *Capella Gallinago* Pleist.–R. Eu. NZ. SA. NA., R. As. Af. Aus., *Limicola Limnocryptes* Pleist.–R. Eu., R. As., *Limnodromus* Pleist.–R. NA., R. EAs., *Arenaria Tringoides* Pleist.–R. Eu., R. As. Af. Aus. NA. SA., *Ereunetes* Pleist.–R. SA., R. NA. EAs., *Philomachus* Pleist.–R. Eu., R. As. Af., *Erolia* Pleist.–R. Eu. NA., R. Cos., *Helodromas* Pleist.–R. Eu., R. As.

EInd. NA. SA. **F. Recurvirostridae,** R. Cos., *Recurvirostra* Pleist.–R. NA., R. Eu. As. Af. Aus. SA. **F. Presbyornithidae,** *Presbyornis* Eoc. NA. **F. Phalaropodidae,** R. Eu. As. NA. Oc., *Lobipes* Pleist.–R. NA., R. Eu. As. Oc. **F. Dromadidae,** R. Ind. Oc. **F. Burhinidae,** R. Eu. As. Af. Aus. CA. SA., *Milnea* Mioc. Eu. **F. Glareolidae,** R. Eu. Af. As. Aus. **F. Thinacoridae,** R. SA. **F. Chionididae,** R. Antarctic Ocean.

SUBORDER LARI. **F. Stercorariidae,** R. Oc. **F. Laridae,** R. Oc., *Limosavis* Eoc. NA., *Halcyornis* Eoc. Eu., ?*Limicolavis* Olig. NA., *Rupelornis* Olig. Eu., *Larus* Olig.–R. Eu. NA., Pleist.–R. As., R. Af. Aus. SA., *Gaviota* Mioc. NA., *Sterna* Plioc.–R. Eu., R. NA. As. Af. Aus. SA., *Ocyplanus* Pleist. Aus., *Xema* Pleist.–R. NA., R. As., ?*Pseudosterna* U. Tert. SA., *Chlidonias* [*Hydrochelidon*] Pleist.–R. Eu. NA., R. Cos. **F. Rynchopidae,** R. NA. SA. Af. SAs.

SUBORDER ALCAE. **F. Alcidae,** R. Eu. As NA. NAtl. NPac. Arc., *Hydrotherikornis Nautilornis* Eoc. NA., *Miocepphus* Mioc. NA., *Cerorhinca* Mioc.–R. NA., R. NPac., *Uria* Mioc.–R. NA., Plioc.–R. Eu., R. NAtl. NPac., *Pliolundia Mancalla* Plioc. NA., *Synthliboramphus* Pleist. NA., R. NAs. NPac., *Cepphus* Pleist.–R. Eu., R. NA. As., *Alca* Pleist.–R. Eu. NA., R. NAtl., *Alle* Pleist.–R. Eu., R. NA. NAtl. Arc., *Fratercula* Pleist.–R. Eu., R. NA. NAtl. NPac.

ORDER COLUMBIFORMES

SUBORDER PTEROCLETES. **F. Pteroclidae,** R. Eu. Af., *Syrrhaptes* Pleist. Eu., Pleist.–R. As.

SUBORDER COLUMBAE. **F. Dididae (Raphidae),** *Didus* [*Raphus*] Subrecent Mauritius, *Pezophaps* Subrecent Rodriguez. **F. Columbidae,** R. Cos., *Gerandia* Mioc. Eu., *Columba* Mioc.–R. Eu., Plioc.–R. NA. As., Pleist. NZ. WInd., R. Af. Aus. SA. Oc., *Lithophaps Progura* Pleist. Aus., *Zenaidura* Pleist.–R. NA., R. SA., *Ectopistes* Pleist.–R. NA., *Homopelia* Pleist.–R. Rodriguez, R. Mad., *Leucosarcia* Pleist.–R. Aus., *Oreopeleia* Pleist.–R. WInd., R. CA. SA., *Zenaida* Pleist.–R. NA. WInd. SA., *Nesoenas* Pleist.–R. Mauritius, *Leptotila Claravis* [*Peristera*] Pleist.–R. SA., R. CA., *Geotrygon* Pleist.–R. SA., R. CA. WInd., *Columbigallina* [*Chamoepelia*] Pleist.–R. SA. WInd., R. NA., *Turtur* Pleist.–R. Eu., R. Af. As.

ORDER PSITTACIFORMES. **F. Psittacidae,** R. NA. SA. Af. SAs. Aus., *Archaeopsittacus* Mioc. Eu., *Conuropsis* Mioc.–R. NA., *Protoconurus* Pleist. SA., *Nestor Strigops* Pleist.–R. NZ., *Brotogerys Microsittace* Pleist.–R. SA., *Aratinga* [*Conurus*] *Amazona* Pleist.–R. SA., R. CA. WInd., *Ara* Pleist.–R. SA. WInd., R. CA., *Coracopsis* Pleist.–R. Mad., *Pyrrhura* Pleist.–R. SA., R. CA., *Rhynchopsitta* Pleist.–R. NA., *Lophopsittacus* Subrecent Mauritius, *Necropsittacus* Subrecent Rodriguez.

ORDER CUCULIFORMES

SUBORDER MUSOPHAGI. **F. Musophagidae,** R. Af.

SUBORDER CUCULI. **F. Cuculidae,** *Dynamopterus* Olig. Eu., *Necrornis* Mioc. Eu., *Neomorphus* Pleist. NA., R. CA. SA., *Coua* Pleist.–R. Mad., *Geococcyx* Pleist.–R. NA., *Capito* Pleist.–R. SA., *Saurothera* Pleist.–R. WInd., *Cuculus* Pleist.–R. Eu. R. Af. As. Aus., *Diplopterus Coccyzus* Pleist.–R. SA., R. NA., *Crotophaga* Pleist.–R. SA. WInd., R. NA., *Piaya* Pleist.–R. SA., R. CA. WInd.

ORDER STRIGIFORMES. **F. Protostrigidae,** *Protostrix* Eoc. NA. **F. Tytonidae,** *Tyto* Pleist.–R. WInd. NA., R. SA. As. Eu. Af. Aus. **F. Strigidae,** *Bubo* Olig.–R. Eu., Pleist.–R. NA. As., R. NAf., *Strigogyps Necrobyas* Olig. Eu., *Asio* Olig.–R. Eu., Pleist.–R. Af. NA. SA. As., R. Aus., *Strix* [*Syrnium*] Mioc.–R. Eu., Pleist.–R. NA. SA., R. As. Af. Aus., *Glaucidium* Plioc.–R. Eu., Pleist.–R. NA. SA., R. As. Af. EInd., *Athene* Plioc.–R. Eu., Pleist. Rodriguez, Pleist.–R. As. CA., *Gymnasio* Pleist.–R. WInd., *Sceloglaux* Pleist.–R NZ., *Aegolius* Pleist.–R. NA. Eu., R. As. SA., *Ketu-*

pa Pleist.-R. As., R. EInd., *Nyctea Surnia* Pleist.-R. Eu., R. As. NA., *Scops Speotyto* Pleist.-R. NA. SA., *Otus* Pleist.-R. NA., R. As. Af. SA. EInd. Eu.

ORDER CAPRIMULGIFORMES

SUBORDER STEATORNITHES. **F. Steatornithidae,** R. SA.

SUBORDER CAPRIMULGI. **F. Podargidae,** R. SAs. EInd. Aus. **F. Nyctibiidae,** R. SA. CA., *Nyctibius* Pleist.-R. SA., R. CA. **F. Aegothelidae,** R. Aus. **F. Caprimulgidae,** R. Cos., *Caprimulgus* Plioc.-R. Eu., Pleist.-R. WInd. SA., R. As. EInd. Af. NA., *Hydropsalis Eleothreptus* Pleist.-R. SA., *Nyctidromus* Pleist.-R. SA., R. NA., *Phalaenoptilus* Pleist.-R. NA.

ORDER MICROPODIFORMES

SUBORDER MICROPODI. **F. Aegialornithidae,** *Aegialornis* Olig. Eu. **F. Micropodidae,** *Cypselavus* Olig.-Mioc. Eu., *?Limnatornis* Mioc. Eu., *Collocalia* Mioc. Eu., R. As. EInd., *Cypselus* Mioc.-R. Eu., Pleist.-R. As., R. Af., *Chaetura* Pleist.-R. SA., R. NA. As. Af. EInd. **F. Hemiprocnidae,** R. SAs. EInd.

SUBORDER TROCHILI. **F. Trochilidae,** R. NA. SA.

ORDER COLIIFORMES. **F. Coliidae,** R. Af.

ORDER TROGONIFORMES. **F. Trogonidae,** R. Af. SAs. Aus. CA. SA., *Archaeotrogon Paratrogon* Olig. Eu., *Trogon* Mioc. Eu., Pleist.-R. SA., R. CA.

ORDER CORACIIFORMES

SUBORDER ALCEDINES. **F. Alcedinidae,** R. Cos., *Alcedo* Pleist.-R. Eu., R. As., *Ceryle* Pleist.-R. SA., R. NA. As. Af. EInd. Eu. **F. Todidae,** R. WInd. **F. Momotidae,** R. CA. SA., *Momotus* Pleist.-R. SA., R. CA.

SUBORDER MEROPES. **F. Meropidae,** R. Af. As. EInd. Aus.

SUBORDER CORACII. **F. Coraciidae,** R. Eu. As. Af. Aus., *Geranopterus* Mioc. Eu., *Coracias* Pleist.-R. Eu., R. As. Af. EInd. **F. Leptosomatidae,** R. Mad. **F. Upupidae,** R. Eu. As. Af. Aus., *Upupa* Pleist.-R. Eu., R. As. Af. Aus. **F. Phoeniculidae,** R. Af.

SUBORDER BUCEROTES. **F. Bucerotidae,** R. Af. SAs. Aus., *?Geisiloceros* Eoc. Eu.

ORDER PICIFORMES

SUBORDER GALBULAE. **F. Galbulidae,** R. CA. SA. **F. Bucconidae,** R. SA. CA., *Bucco* Pleist.-R. SA., *Malacoptila* Pleist.-R. SA., R. CA. **F. Capitonidae,** R. SA. Af. SAs. Aus. **F. Indicatoridae,** R. Af. As. Aus. **F. Ramphastidae,** R. SA. CA., *Ramphastos* Pleist.-R. SA., R. CA.

SUBORDER PICI. **F. Picidae,** R. Eu. As. Af. EInd. NA. SA., *?Cryptornis* Eoc. Eu., *? Uintornis* Eoc. NA., *Palaeopicus ?Homalopus* Mioc. Eu., *Picus* Mioc.-R. Eu., R. As., *Dendrocopos* Plioc.-R. Eu., R. As. NAf. NA. CA., *Iynx* Plioc.-R. Eu., R. As. Af., *Dendrocoptes* Plioc.-R. Eu., R. WAs., *Coephloeus* Pleist. NA., R. CA. SA., *Leuconerpes Chrysoptilus* Pleist.-R. SA., *Gecinus* Pleist.-R. Eu., R. As. EInd. NAf., *Asyndesmus* Pleist.-R. NA., *Colaptes* Pleist.-R. NA. SA., *Melanerpes* Pleist.-R. WInd. SA., R. NA.

ORDER PASSERIFORMES

SUBORDER EURYLAIMI. **F. Eurylaimidae,** R. SAs. EInd.

SUBORDER TYRANNI. **F. Dendrocolaptidae,** R. SA. CA., *Picolaptes Xiphocolaptes* Pleist.-R. SA., R. CA. **F. Furnariidae,** R. NA. SA., *Synallaxis Furnarius* Pleist.-R. SA. **F. Formicariidae,** R. CA. SA., *Chamaeza* Pleist.-R. SA. **F. Conopophagidae,** R. SA. **F. Rhinocryptidae,** R. CA. SA. **F. Cotingidae,** R. NA. SA. *Procnias* Pleist-R. SA. **F. Pipridae,** R. CA. SA. **F. Tyrannidae,** R. NA. SA., *Tolmarchus* Pleist.-R. WInd., *Tyrannus Myriarchus Blacicus* Pleist.-R. WInd., R. NA. SA. **F. Oxyrun-**

cidae, R. CA. SA. F. **Phytotomidae**, R. SA. F. **Pittidae**, R. Af. SAs. Aus. F. **Acanthisittidae**, R. NZ. F. **Philepittidae**, R. Mad.

SUBORDER MENURAE. F. **Menuridae**, R. Aus. F. **Atrichornithidae**, R. Aus.

SUBORDER PASSERES. F. **Alaudidae**, R. Cos., *Alauda* Plioc.–R. Eu., Pleist.–R. As., R. NAf., *Otocorys* Pleist.–R. Eu. NA., R. As. NAf., *Galerida* Pleist.–R. Eu. As., R. Af., *Lullula* Pleist.–R. Eu., R. WAs. F. **Palaeospizidae**, *Palaeospiza* Mioc. NA. F. **Hirundinidae**, R. Cos., *Hirundo* Plioc.–R. Eu., Pleist.–R. As. SA., R. NA. Af. Aus., *Riparia* Pleist.–R. Eu., R. As. NA. SA., *Petrochelidon* Pleist.–R. NA. WInd., R. SA. Af. As. Aus., *Chelidon* Pleist.–R. Eu., R. As. Af. EInd. F. **Campephagidae**, R. Eu. As. Af. Aus. F. **Dicruridae**, R. Af. SAs. Aus. F. **Oriolidae**, R. Eu. As. Af. Aus., *Oriolus* Pleist.–R. Eu., R. As. EInd. Af. F. **Corvidae**, R. Cos., *Miocorax* Mioc. Eu., *Corvus* Mioc.–R. Eu., Pleist.–R. NA. WInd. As., R. Af. Aus., *Pyrrhocorax* Plioc.–R. As., Pleist.–R. Eu., *Coloeus* Pleist.–R. Eu., R. As., *Pica* Pleist.–R. Eu. NA. As., R. NAf., *Nucifraga* Pleist.–R. Eu., R. As. NA., *Garrulus* Pleist.–R. Eu., R. As. NAf., *Cyanocorax* Pleist–R. SA., *Cyanocitta Aphelocoma Cyanocephalus* Pleist.–R. NA., *Palaeocorax* Pleist. NZ. F. **Paradiseidae**, R. EInd. Aus. F. **Paradoxornithidae**, R. EInd. Aus. F. **Paridae**, R. Eu. As. Af. NA., *Palaegithalus* Eoc. Eu., *Parus* Plioc.–R. Eu., R. As. EInd., *Aegithalus* Plioc.–R. Eu., R. As., *Penthestes* Pleist.–R. NA. F. **Sittidae**, R. Eu. As. Aus. NA. Mad., *Sitta* Plioc.–R. Eu., Pleist.–R. NA., R. As. F. **Hyposittidae**, R. Mad. F. **Certhiidae**, R. Eu. As. NA. Aus., *Certhia* Plioc.–R. Eu., R. As. NA. F. **Chamaeidae**, R. NA., *Chamaea* Pleist.–R. NA. F. **Timaliidae**, R. Eu. As. Af. Aus., *Pterorhinus* Pleist.–R. As. F. **Pycnonotidae**, R. Eu. As. Af. Aus. NA. SA., *Pycnonotus* Pleist.–R. As., R. Af. EInd. F. **Cinclidae**, R. Eu. As. NA., *Cinclus* Pleist.–R. Eu., R. As. NA. SA. F. **Troglodytidae**, R. Eu. As. EInd. NA. SA., *Troglodytes* Pleist. Eu., R. NA. SA. F. **Mimidae**, R. NA. SA., *Mimus* Pleist.–R. WInd. SA., R. NA., *Margarops* Pleist. WInd., *Oreoscoptes Toxostoma* Pleist.–R. NA. F. **Turdidae**, R. Cos., *Pratincola* Plioc.–R. Eu., R. As. Af., *Monticola* Plioc.–R. Eu., R. As. NAf., *Turdus* Plioc.–R. Eu., Pleist.–R. As. SA. NA., *Mimocichla* Pleist.–R. WInd., *Sialia* Pleist.–R. NA., *Saxicola* Pleist.–R. Eu., R. Af. As. NA., *Phoenicurus* Pleist.–R. Eu., R. As Af., *Erithacus Luscinia* Pleist.–R. Eu., R. As. F. **Zeledoniidae**, R. CA. F. **Sylviidae**, R. Eu. As. Af. Aus. Oceania, *Sylvia* Olig.–R. Eu., R. As. Af., *Phylloscopus* Pleist.–R. Eu. As., R. Af., *Locustella* Pleist.–R. Eu., R. As. EInd. NAf., *Acrocephalus* Pleist.–R. Eu., R. As. Af. Aus. Oceania F. **Regulidae**, R. Eu. NAf. As. NA., *Regulus* Pleist.–R. Eu., R. NAf. As. NA. F. **Muscicapidae**, R. Eu. As. Af. Aus. F. **Prunellidae**, R. Eu. As., *Prunella* Pleist.–R. Eu., R. As. F. **Motacillidae**, R. Cos., *Anthus* Plioc.–R. Eu., R. Af. As. Aus. NA. SA., *Motacilla* Mioc.–R. Eu., Pleist.–R. As., R. NAf. NA. F. **Bombycillidae**, R. Eu. As. NA., *Bombycilla* Pleist. Eu. NA., R. As. F. **Ptilogonatidae**, R. CA. SA. F. **Dulidae**, R. WInd. F. **Artamidae**, R. Af. SAs. Aus. F. **Vangidae**, R. Mad. F. **Laniidae**, R. Eu. As. Af. Aus. NA., *Laurillardia* Eoc. Eu., *Lanius* Mioc.–R. Eu., Pleist.–R. NA., R. As. Af. F. **Prionopidae**, R. Af. SAs. Aus. F. **Cyclarhidae**, R. CA. SA. F. **Vireolaniidae**, R. CA. SA. F. **Sturnidae** (incl. **Graculidae**), R. Eu. As. Af. Aus., *Sturnus Pastor* Pleist.–R. Eu., R. As., *Hetarolocha Necropsar* Pleist. Rodriguez, Pleist.–R. NZ. F. **Melithreptidae**, R. Aus. F. **Nectariniidae**, R. Af. SAs. Aus. F. **Dicaeidae**, R. Af. SAs. Aus. F. **Zosteropidae**, R. Af. As. Aus. F. **Vireonidae**, R. NA. SA., *Vireosylva* Pleist.–R. WInd., R. NA. SA. F. **Coerebidae**, R. CA. SA. WInd., *Coereba* Pleist.–R. WInd., R. CA. SA. F. **Drepanididae**, R. Hawaiian Is. F. **Compsothlypidae**, R. NA. SA., *Mniotilta Dendroeca* Pleist.–R. WInd., R. NA. SA. F. **Ploceidae**, R. Eu. As. Af. Aus. *Passer* Olig.–R. Eu., Pleist.–R. As., R. Af. EInd. F. **Icteridae**, R. NA.

SA., *Pyelorhampus* Pleist. NA., *Agelaius* Pleist–R. NA. WInd., R. SA., *Icterus* Pleist.–R. WInd., R. NA. SA., *Sturnella* Pleist.–R. NA., R. SA., *Xanthocephalus Quiscalus* Pleist.–R. NA., *Cassicus* Pleist.–R. SA., R. CA., *Euphagus Cassidix* [*Megaquiscalus*] Pleist.–R. NA., R. CA., SA. *Pseudoleistes Aphobus* Pleist.–R. SA. **F. Tersinidae,** R. NA. SA. **F. Thraupidae,** R. NA. SA., *Spindalis* Pleist.–R. WInd., *Holoquiscalus* Pleist.–R. WInd., R. SA. **F. Catamblyrhynchidae,** R. SA. **F. Fringillidae,** R. Cos., *Fringilla* Mioc.–R. Eu., ?Plioc. NA., Pleist.–R. As., R. NAf., *Palaeostruthus* Plioc. NA., *Spinus* Pleist.–R. NA., R. SA. Eu. As. Af., *Junco Amphispiza Passerella Pipilo Spizella* Pleist.–R. NA., *Saltator* Pleist.–R. SA., R. CA. WInd., *Montifringilla Pinicola Plectrophenax* Pleist.–R. Eu., R. As. NA., *Coccothraustes* Pleist.–R. Eu. As., R. NAf., *Carduelis* Pleist.–R. Eu., R. NAf. WAs., *Linaria* Pleist.–R. Eu., R. As. NAf. NA., *Serinus* Pleist.–R. Eu., R. Af. WAs., *Pyrrhula Chloris* Pleist.–R. Eu., R. As., *Loxia* Pleist.–R. Eu. NA., R. NAf. As., *Emberiza* Pleist.–R. Eu. As., R. Af., *Carpodacus* Pleist.–R. As., R. Eu. NA., *Loxigilla Tiaris* Pleist.–R. WInd., *Coturniculus* Pleist.–R. WInd., R. NA.

PASSERIFORMES INCERTAE SEDIS. *Protornis* Eoc. Eu., *Hebe* Eoc. NA., *Fontinalis* Mioc. NA.

Aves Incertae Sedis. *?Laopteryx* U. Jur. NA., *Eopteryx* Eoc. NA.

CLASS MAMMALIA

SUBCLASS PROTOTHERIA

Order Monotremata. **F. Ornithorhynchidae,** R. Aus., *Ornithorhynchus* Pleist.–R. Aus. **F. Echidnidae (Tachyglossidae),** R. Aus., *Echidna* [*Tachyglossus*] Pleist.–R. Aus.

SUBCLASS THERIA

INFRACLASS UNCERTAIN

Order Triconodonta. **F. Triconodontidae,** *Amphilestes Phascolotherium* M. Jur. Eu., *Triconodon* U. Jur. Eu., *Trioracodon* U. Jur. Eu. NA., *Aploconodon Phascolodon Priacodon* U. Jur. NA.

Order Symmetrodonta. **F. Spalacotheriidae,** *Peralestes Spalacotherium* U. Jur. Eu. **F. Amphidontidae,** *Amphidon ?Eurylambda Tinodon* U. Jur. NA., *Manchurodon* Jur. As.

INFRACLASS ALLOTHERIA

Order Multituberculata. **F. Plagiaulacidae,** *Bolodon Plagiaulax* U. Jur. Eu., *Ctenacodon* U. Jur. Eu. NA., *Psalodon* U. Jur. NA., *Loxaulax* L. Cret. Eu. **F. Ptilodontidae,** *Cimolomys Essonodon Meniscoëssus Paronychodon* U. Cret. NA., *Djadochtatherium* U. Cret. As., *Ancomodon Kimbetohia Litotherium Mesodma Microcosmodon Parectypodus Pentacosmodon Ptilodus* Paleoc. NA., *Liotomus Neoctenodon Neoplagiaulax* Paleoc. Eu., *Ectypodus Eucosmodon Neoliotomus Prochetodon* Paleoc.–Eoc. NA. **F. Taeniolabidae,** *Catopsalis Taeniolabis* [*Polymastodon*] Paleoc. NA., *Prionessus Sphenopsalis* Paleoc. As.

INFRACLASS PANTOTHERIA

Order Pantotheria (Trituberculata). **F. Amphitheriidae,** *Amphitherium* M. Jur. Eu. **F. Dryolestidae,** *Dryolestes Euthlastes Herpetairus Kepolestes Laolestes Malthacolestes Melanodon Miccylotyrans Pelicopsis* U. Jur. NA., *Kurtodon Peraspalax Phascolestes* U. Jur. Eu., *Amblotherium* U. Jur. Eu. NA. **F. Paurodontidae,** *Brancatherulum* U. Jur. Af., *Araeodon Archaeotrigon Paurodon Tathiodon* U. Jur. NA., *Peramus* U. Jur. Eu. **F. Docodontidae,** *Dicrocynodon Docodon Enneacodon* U. Jur. NA., *Peraiocynodon* U. Jur. Eu.

INFRACLASS METATHERIA

ORDER MARSUPIALIA

SUBORDER POLYPROTODONTA. **F. Didelphidae,** R. NA. SA., *Alphodon Cimolestes Delphodon Diaphorodon Didelphodon Ectoconodon Eodelphis Euangelistes Nyssodon Pediomys Thaelodon* U. Cret. NA., *Peradectes Thylacodon* Paleoc. NA., ?*Gashternia* Paleoc. SA., *Adapisoriculus* Paleoc. Eu., *Coona Ideodelphis* Eoc. SA., *Peratherium* Eoc.–Mioc. Eu. NA., *Nanodelphys* Olig. NA., *Microbiotherium* Olig.–Mioc. SA., *Hyperdidelphys Notictis Oligobiotherium Pachybiotherium Prodidelphys Stylognathus* Mioc. SA., *Cladodidelphys Paradidelphys* Plioc. SA., *Lutreolina* Plioc.–R. SA., *Didelphis* Plioc.–R. SA., Pleist.–R. NA., *Caluromys Chironectes Marmosa Metachirus Peramys* Pleist.–R. SA. **F. Caroloameghiniidae,** *Caroloameghinia* Eoc. SA. **F. Borhyaenidae,** *Patene* Paleoc.–Eoc. SA., *Arminiheringia Dilestes Pseudocladosictis* Eoc. SA., *Procladosictis* Eoc.–Olig. SA., *Notogale Pharsophorus Proborhyaena* Olig. SA., *Borhyaena Cladosictis* Olig.–Mioc. SA., *Acrocyon Agustylus Apera Conodonictis Ictioborus Lycopsis Napodonictis Perathereutes Prothylacinus Pseudoborhyaena Pseudothylacinus Sipalocyon Thylacodictis* [*Amphiproviverra*] Mioc. SA., *Achlysictis Acrohyaenodon Hyaenodonops Notocynus Parahyaenodon Perazoyphium Sparassocynus Stylocynus Thylacosmilus* Plioc. SA. **F. Dasyuridae,** R. Aus., *Dasyurus Phascogale Sarcophilus Thylacinus* Pleist.–R. Aus. **F. Notoryctidae,** R. Aus. ?**F. Necrolestidae,** *Necrolestes* Mioc. SA. **F. Peramelidae,** R. Aus., *Isoödon Perameles Paragalia* Pleist.–R. Aus.

SUBORDER CAENOLESTOIDEA. **F. Polydolopidae,** *Seumadia* Paleoc. SA., *Polydolops* Paleoc.–Eoc. SA., *Amphidolops Anadolops Anissodolops Archaeodolops Eudolops Odontomysops Orthodolops Pliodolops Promysops Propolymastodon Pseudolops* Eoc. SA. **F. Caenolestidae,** R. SA., *Progarzonia* Eoc. SA., *Micrabderites Palaeepanorthus Pitheculites Pseudhalmarhiphus* Olig. SA., *Abderites Callomenus Garzonia Parabderites Pilchenia* Olig.–Mioc. SA., *Acdectis Decastis Dipilus* ?*Eomannodon Essoprion Halmadromus Halmarhiphus Halmaselus* ?*Mannodon Metriochomus Palaeothentes* [*Epanorthus*] *Parhalmarhiphus Pichipilus Prepanorthus Stilotherium Tideus* Mioc. SA., *Zygolestes* Plioc. SA.

SUBORDER DIPROTODONTA. **F. Phalangeridae,** R. Aus., *Wynyardia* Mioc. Aus., *Archizonurus Burramys Koalemus Palaeopetaurus* Pleist. Aus., *Cuscus Dromicia Petaurus Pseudochirus Trichosurus* Pleist.–R. Aus., *Phalanger* Pleist.–R. EInd., R. Aus. **F. Macropodidae,** R. Aus., *Brachalletes Palorchestes Procoptodon Propleopus Protemnodon Sthenurus Synaptodon* Pleist. Aus., *Aepyprymnus Bettongia Macropus Petrogale Potorous* [*Hypsiprymnodon*] *Thylogale* Pleist.–R. Aus. **F. Phascolomyidae,** R. Aus., *Phascolonus* Pleist. Aus., *Phascolarctos Phascolomys* Pleist.–R. Aus. **F. Diprotodontidae,** *Diprotodon Euowenia Euryzygoma Nototherium Stheronerus Zygomaturus* Pleist. Aus. **F. Thylacoleontidae,** *Thylacoleo* Pleist. Aus.

INFRACLASS EUTHERIA

ORDER INSECTIVORA

SUBORDER ZALAMBDODONTA

SUPERFAMILY DELTATHERIDIOIDEA. **F. Deltatheridiidae,** *Deltatheridium Deltatheroides Hyotheridium* U. Cret. As., *Acmeodon Gelastops Puercolestes* Paleoc. NA., *Didelphodus Phenacops* Eoc. NA.

SUPERFAMILY CENTETOIDEA. **F. Palaeoryctidae,** *Palaeoryctes* Paleoc. NA. **F. Solenodontidae,** R. WInd., *Apternodus Clinopternodus Micropternodus* Olig. NA. **F. Centetidae,** R. Mad., *Centetes* [*Tenrec*] *Microgale* Pleist.–R. Mad. **F. Potamogalidae** R. WAf.

SUPERFAMILY CHRYSOCHLOROIDEA. F. **Chrysochloridae,** R. SAf., ? *Arctoryctes* Mioc. NA., *Proamblysomus* Pleist. SAf., *Chlorotalpa* Pleist.–R. SAf.

SUBORDER DILAMBDODONTA

SUPERFAMILY ERINACEOIDEA. **F. Zalambdalestidae,** *Zalambdalestes* U. Cret. As. **F. Leptictidae,** *Gypsonictops* U. Cret. NA., ?*Acmeodon Emperodon Leptacodon* ? *Litolestes Myrmecoboides Prodiacodon* [*Palaeolestes*] ?*Xenacodon* Paleoc. NA., ? *Praolestes* ? *Pseudictops* Paleoc. As., *Diacodon* Paleoc.–Eoc. NA., *Adapisorex* Paleoc.–Eoc. Eu., *Parictops Protictops* Eoc. NA., *Ictops Leptictis* Olig. NA. **F. Dimylidae,** *Cordylodon Dimylus Metacordylodon Plesiodimylus* Mioc. Eu. **F. Erinaceidae,** R. As. Af., *Entomolestes Proterixoides* Eoc. NA., *Necrogymnurus* Eoc.–Olig. Eu., *Palaeoerinaceus* Eoc.–Mioc. Eu., Mioc. Af., *Metacodon Proterix* Olig. NA., *Tetracus* Olig. Eu., *Palaeoscaptor Tupaiodon* Olig. As., *Brachyerix Parvericius* Mioc. NA., *Galerix Lanthanotherium Parasorex Pseudogalerix* Mioc. Eu., *Metechinus* Mioc.–Plioc. NA., *Erinaceus* Mioc.–R. Eu., Pleist.–R. As. NAf., *Meterix* Plioc. NA.

SUPERFAMILY SORICOIDEA. **F. Nyctitheriidae,** *Protentomodon Stilpnodon* Paleoc. NA., *Centetodon Myolestes Nyctitherium* Eoc. NA. **F. Soricidae,** R. Eu. As. Af. NA., *Saturninia* Eoc. Eu., *Macrosorex Plesiosorex* Olig. Eu., *Protosorex* Olig. NA., *Limnoecus* Mioc. NA., *Heterosorex Trimylus* Mioc. Eu., *Sorex* Mioc.–R. Eu., Plioc.–R. NA., Pleist.–R. As., *Crocidura* Mioc.–R. Eu., Pleist.–R. As. Af., *Mystipterus* Plioc. NA., *Blarina* Plioc.–R. NA., *Anourosorex* Plioc.–R. As., *Blarinella* Plioc.–R. As., Pleist. Eu., *Beremendia* Pleist. Eu., *Soriculus* Pleist.–R. Eu. Af., *Neomys* Pleist.–R. Eu. As., *Cryptotis Microsorex* Pleist.–R. NA. **F. Talpidae,** R. Eu. As. NA., *Amphidozotherium* Eoc.–Olig. Eu., *Geotrypus* Olig. Eu., *Geolabis* Olig. NA., *Proscalops* Olig.–Mioc. NA., *Proscapanus Scaptogale* [*Echinogale*] Mioc. Eu., *Talpa* Mioc. NA., Mioc.–R. Eu., Pleist.–R. As., *Desmana* [*Mygale*] Mioc.–R. Eu., R. As., *Scaptonyx* Mioc. Eu., R. As., *Hesperoscalops* Plioc. NA., *Scalopus Scapanus* Plioc.–R. NA., *Scapanulus* Plioc.–R. As., *Scaptochirus* Pleist.–R. As., *Parascalops* Pleist.–R. NA. **F. Nesophontidae,** *Nesophontes* Pleist. WInd.

SUPERFAMILY PANTOLESTOIDEA. **F. Pantolestidae,** *Aphronorus Bessoecetor Pentacodon Propalaeosinopa* Paleoc. NA., *Palaeosinopa* Paleoc.–Eoc. NA., Eoc. Eu., *Pantolestes* Eoc. NA.

SUPERFAMILY MACROSCELIDOIDEA. **F. Macroscelididae,** R. Af., ? *Pseudorhynchocyon* Olig. Eu., *Elephantulus Macroscelides* Pleist.–R. Af.

SUBORDER MIXODECTOIDA. **F. Mixodectidae,** *Dracontolestes Eudaemonema Elpidophorus Indrodon Mixodectes* ? *Unuchinia* Paleoc. NA., *Craseops Cynodontomys Microsyops* Eoc. NA.

SUBORDER DERMOPTERA. **F. Plagiomenidae,** *Planetetherium* Paleoc. NA., *Plagiomene* Eoc. NA. **F. Galeopithecidae,** R. EInd.

INSECTIVORA INCERTAE SEDIS. *Apheliscus* ? *Coriphagus Megapterna Picrodus Zanycteris* Paleoc. NA.

ORDER CHIROPTERA

SUBORDER MICROCHIROPTERA. **F. Rhinopomidae,** R. As. Af. **F. Emballonuridae,** R. SA. CA. Af. As. Aus., *Vespertiliavus* Eoc.–Olig. Eu., *Taphozous* ?Eoc., Olig. Eu., Pleist.–R. SAs., R. Af. Aus., *Saccopteryx* Pleist.–R. SA. **F. Noctilionidae,** R. CA. SA. WInd. **F. Nycteridae,** R. Af. EInd. **F. Megadermidae,** R. Af. SAs. EInd. Aus., *Necromantis* Eoc.–Olig. Eu., *Megaderma* ?Mioc. Eu., Pleist.–R. As., R. EInd. **F. Rhinolophidae,** R. Eu. Af. SAs. Aus., *Rhinolophus* Eoc.–R. Eu., Pleist.–R. SAs., R. Aus., *Palaeonycteris* Olig. Eu. **F. Hipposideridae,** R. Af. SAs. Aus., *Palaeophyllophora* Eoc.–Olig. Eu., *Paraphyllophora Pseudorhinolophus* Eoc.–Mioc. Eu., *Asellia* Pleist.–R. WAs. Mad., R. Af. **F. Phyllostomatidae,** R. NA. SA., ?*Paleurycteris* Eoc. Eu., *Provampyrus Vampyravus* Olig. Af., *Brachyphylla Erophylla Macrotus Monophyllus Phyllonycteris Phyllops Stenoderma* Pleist.–R. WInd., *Artibeus Chilonycteris Mormoöps* Pleist.–R. WInd., R. SA., *Anthorhina Carollia Chiroderma Chrotopterus Glossophaga Lonchoglossa Micronycteris Phyllostomus Pygoderma Sturnira Vampyrops* Pleist.–R. SA. **F. Desmodontidae,** R. SA. CA., *Desmodus* Pleist.–R. SA., R. CA. **F. Natalidae,** R. SA. CA., *Natalus* Pleist.–R. SA., R. CA. **F. Furipteridae,** R. SA. **F. Thyropteridae,** R. SA. CA. **F. Myzopodidae,** R. Mad. **F. Vespertilionidae,** R. Cos., *Nycterobius* Eoc.–Olig. Eu. *Myotis* Olig.–R. Eu., Pleist.–R. As. NA., R. NAf. EInd. Aus., *Vespertilio* Mioc.–R. Eu., Pleist.–R. NA., *Samonycteris* Plioc. WAs., *Pipistrellus* Plioc.–R. NA., Pleist.–R. Eu., R. As. NAf. EInd. Aus., *Simonycteris* Pleist. NA., *Antrozous* Pleist.–R. NA. WInd., *Corynorhinus* Pleist.–R. NA., *Eptesicus* Pleist.–R. NA. SA. Eu., R. Af. As. Aus., *Histiotus* Pleist.–R. SA., *Lasiurus* Pleist.–R. SA., R. NA. *Barbastella* Pleist.–R. Eu. NAf. WAs., *Miniopterus* Pleist.–R. Eu. *Cyprus*, R. NAf. As., *Plecotus* Pleist.–R. Eu. As., R. NAf. **F. Mystacopidae,** R. NZ. **F. Molossidae,** R. Cos., *Nyctinomus* [*Tadaria*] Mioc.–R. Eu., Pleist.–R. NA. WInd., R. SA. Af. SAs. EInd. Aus., *Molossus* Pleist.–R. NA. SA. **Microchiroptera incertae sedis:** *Archaeonycteris Cecilionycteris, Palaeochiropteryx Paradoxonycteris* Eoc. Eu., *Alastor* Eoc.–Olig. Eu.

SUBORDER MEGACHIROPTERA. **F. Pteropodidae,** R. As. Af. Aus., *Archaeopteropus* Olig. Eu., *Rousellus* Mioc. Eu., R. Af. SAs. EInd., *Pteropus* Pleist.–R. Mad. EInd. R. SAs., Aus.

ORDER TILLODONTIA. **F. Tillotheriidae,** *Esthonyx* Paleoc.–Eoc. NA., Eoc. Eu., *Anchippodus Tillotherium Trogosus* Eoc. NA.

ORDER TAENIODONTIA. **F. Stylinodontidae,** *Conoryctella Conoryctes Onychodectes Wortmania* Paleoc. NA., *Psittacotherium* Paleoc.–Eoc. NA., *Ectoganus Calamodon Stylinodon* Eoc. NA.

ORDER PRIMATES

SUBORDER LEMUROIDEA. **F. Anagalidae,** *Anagale* Olig. As. **F. Tupaiidae,** R. EInd. **F. Plesiadapidae,** *Chiromyoides* Paleoc. Eu., *Pronothodectes* Paleoc. NA., *Plesiadapis* [*Nothodectes*] Paleoc. Eu., Paleoc. ?Eoc. NA., *Platychoerops Megachiromyoides* Eoc. Eu. **F. Adapidae,** *Adapis Amphilemur Anchomomys Caenopithecus ?Ceciliolemur ?Europolemur Pronycticebus Protoadapis* Eoc. Eu., ? *Adapidium* Eoc. As., *Aphanolemur Notharctus Pelycodus* Eoc. NA. **F. Lemuridae,** R. Mad., *Archaeoindris Archaeolemur Hadropithecus Megaladapis Megalindris Mesopropithecus Neopropithecus Nesopithecus Palaeopropithecus Peloriadapis Prohapalemur* Pleist. Mad., *Avahis Cheirogaleus Indris Lemur Lepilemur Propithecus* Pleist.–R. Mad. **F. Chiromyidae,** R. Mad., *Chiromys* [*Daubentonia*] Pleist.–R. Mad. **F. Lorisidae,** R. SAs. Af., *Progalago* Mioc. Af., *Indraloris* Plioc. SAs.

SUBORDER TARSIOIDEA. **F. Anaptomorphidae,** *Navajovius Palaechthon Palenochtha Paromomys Plesiolestes* Paleoc. NA., ?*Phenacolemur* Paleoc.–Eoc. NA., *Absarokius Anaptomorphus Chumashius Dyseolemur Euryacodon Hemiacodon Loveina Omomys Paratetonius Shoshonius Tetonius ?Trogolemur Uintanius ?Uintasorex Washakius Yumanius* Eoc. NA., ?*Megatarsius Microchoerus ?Microtarsioides Necrolemur Periconodon Pseudoloris Teilhardina* Eoc. Eu., ?*Hoanghonius* ?Eoc. As., ?*Macrotarsius* Olig. NA. **F. Tarsiidae,** R. EInd. **F. Carpolestidae,** *Carpodaptes Carpolestes Elphidotarsius* Paleoc. NA. **F. Apatemyidae,** *Jepsenella Labi-*

dolemur Paleoc. NA., *Apatemys Stehlinella Teilhardella* Eoc. NA., *Eochiromys Heterohyus* [*Necrosorex*] Eoc. Eu., *Sinclairella* Olig. NA.

SUBORDER ANTHROPOIDEA

INFRAORDER PLATYRRHINI. F. **Hapalidae,** R. SA., *Hapale* Pleist.–R. SA. F. **Cebidae,** R. SA., *Homunculus ?Pitheculus* Mioc. SA., *Alouatta* [*Mycetes*] *Brachyteles* [*Eriodes*] *Callicebus* [*Callithrix*] *Cebus* Pleist.–R. SA.

INFRAORDER CATARRHINI. F. **Cercopithecidae,** R. As. Af. EInd., *Apidium Moeripithecus Parapithecus* Olig. Af., *Lybipithecus* Plioc. Af., *Dolichopithecus Oreopithecus* Plioc. Eu., *Mesopithecus* ?Mioc. Af., Plioc. Eu. WAs., *Cercopithecus* Plioc. As., R. Af., *Macacus* Plioc.–Pleist. Eu., Plioc.–R. As., Pleist.–R. NAf., R. EInd., *Bunopithecus Procynocephalus* Pleist. As., *Papio* [*Cynocephalus Simopithecus*] Pleist. As., Pleist.–R. Af., *Dinopithecus Parapapio* Pleist. Af., *Semnopithecus* [*Pithecus*] Pleist. Af., Pleist.–R. As., R. EInd., *Cercocebus* Pleist.–R. Af., *Rhinopithecus* Pleist.–R. As. F. **Simiidae,** R. Af. SAs., *? Amphipithecus ?Pondaungia* Eoc. As., *Propliopithecus* Olig. Af., *Dryopithecus* ?Mioc. Af., Mioc.–Plioc. Eu., *Limnopithecus Proconsul Xenopithecus* Mioc. Af., *Pliopithecus* [*Prohylobates*] Mioc. Af., Mioc.–Plioc. Eu., *Austricopithecus* Mioc. Eu., *Paidopithex* Plioc. Eu., *? Adaetontherium Bramapithecus Hylopithecus Ramapithecus Sivapithecus* [*Palaeosimia, Palaeopithecus*] *Sugrivapithecus* Plioc. As., *Gigantopithecus* Pleist. As., *Simia* [*Pongo*] Pleist. As., R. EInd., *Australopithecus* [*Paranthropus Plesianthropus*] Pleist. Af. F. **Hominidae,** R. Cos., *Homo* [*Pithecanthropus Sinanthropus Eoanthropus Palaeanthropus*] Pleist.–R. Eu. As. Af. Aus., R. NA. SA.

ORDER CARNIVORA

SUBORDER CREODONTA

INFRAORDER PROCREODI. F. **Arctocyonidae,** *Baioconodon Carcinodon Claenodon Deltatherium Deuterogonodon Elphidophorus Eoconodon Goniacodon Loxolophus Metachriacus Oxyclaenus Paradoxodon Prothryptacodon Protogonodon Spanoxyodon Tricentes Triisodon* Paleoc. NA., *Arctocyon Arctocyonides* Paleoc. Eu., *Hyracolestes* Paleoc. As., *Chriacus Thryptacodon* Paleoc.–Eoc. NA., *Anacodon* Eoc. NA., *?Paroxyclaenus* Eoc. Eu., *? Ardynictis ?Didymoconus* Olig. As.

INFRAORDER ACREODI. F. **Mesonychidae,** *Microclaenodon* Paleoc. NA., *Dissacus* Paleoc.–Eoc. Eu. NA., *Harpagolestes Mesonyx* Eoc. NA., *Pachyaena Synoplotherium* [*Dromocyon*] Eoc. Eu. NA., *Hapalodectes* Eoc. NA. As., *Andrewsarchus ?Olsenia* Eoc. As.

INFRAORDER PSEUDOCREODI. F. **Oxyaenidae,** *Dipsalodon* Paleoc. NA., *?Sarcodon* Paleoc. As., *Oxyaena* Paleoc.–Eoc. NA., *Ambloctonus Dipsalidictidess Patriofeli Protopsalis* Eoc. NA., *Palaeonictis* Eoc. Eu. NA., *Paroxyaena* Eoc. Eu., *Sarkastodon* Eoc. As. F. **Hyaenodontidae** *?Opisthopsalis* Paleoc. As., *Hyaenodictis* Paleoc.–Eoc. Eu., *Apataelurus Limnocyon Machaeroides Oxyaenodon Prolimnocyon Thinocyon Tritemnodon* Eoc. NA., *Pachyaena Prorhyzaena Thereutherium* Eoc. Eu., *Sinopa* Eoc. Eu. NA., *Paracynohyaenodon Propterodon* Eoc. Eu. As., *Pterodon* Eoc. As. NA., Eoc.–Olig. Eu., Olig.–Mioc. Af., *Cynohyaenodon Galethylax Quercytherium* Eoc.–Olig. Eu., *Hyaenodon* Eoc.–Olig. Eu. NA. As., Olig.–Mioc. Af., *?Dyspterna* Olig. Eu., *Hemipsalodon* Olig. NA., *Metasinopa ?Ptolemaia* Olig. Af., *Apterodon* [*Dasyurodon*] Olig. Eu. As., Olig.–Mioc. Af., *Metapterodon* Mioc. Af., *Dissopsalis* Plioc. As.

SUBORDER FISSIPEDIA

INFRAORDER EUCREODI. F. **Miacidae,** *Ictidopappus* Paleoc. NA., *Didymictis* Paleoc.–Eoc. NA., *Mimocyon Oödectes Palaearctonyx Pleurocyon Tapocyon Uintacyon*

Vassocyon Vulpavus Eoc. NA., ?*Proviverra* Eoc. Eu., *Miacis* Eoc. NA. Eu. As., *Viverravus* Eoc. NA. Eu. ?As.

INFRAORDER AELUROIDEA. **F. Viverridae**, R. Af. SAs. Eu. EInd., *Stenogale Stenoplesictis* Eoc.–Olig. Eu., *Palaeoprionodon* Eoc.–Olig. Eu., Olig. As., *Proailurus* Eoc.–Mioc. Eu., *Amphicticeps* Olig. As., *Herpestes* ?Olig. Mioc.–R. Eu., Mioc.–R. Af., Pleist.–R. As., *Viverra* ?Olig., Mioc.–R. Eu., Plioc.–R. As., Pleist.–R. Af., *Leptoplesictis Semigenetta* Mioc. Eu., *Tungurictis* Mioc. As., *Progenetta* Mioc.–Plioc. Eu., *Vishnuictis* Plioc. As., *Paguma* Pleist.–R. As., *Atilax Crossarchus Suricata* Pleist.–R. Af., *Genetta* Pleist.–R. Af., R. WAs. Eu., *Cryptoprocta Fossa* Pleist.–R. Mad., *Paradoxurus* Pleist.–R. EInd. **F. Hyaenidae**, R. Af. SAs., *Crocuta* Mioc.–Pleist. As., Plioc.–Pleist. Eu., R. Af., *Hyaena* Plioc.–R. As., Plioc.–Pleist Eu., Pleist.–R. Af., ?*Chasmaporthetes* Plioc. NA., *Ictitherium Lycaena* Plioc. Eu. As., *Hyaenictis* Plioc. Eu., Pleist. As. **F. Felidae**, R. Eu. As. Af. EInd. NA. SA., *Aelurictis* Eoc.–Olig. Eu., *Eusmilus* Eoc.–Olig. Eu., Olig. NA., *Dinailurictis* Olig. Eu., *Dinictis* Olig. NA., *Hoplophoneus Nimravus* Olig.–Mioc. NA., *Archaelurus Dinaelurus Pogonodon* Mioc. NA., ?*Hyaenailurus* Mioc. As., *Pseudaelurus* Mioc. Eu. Af. NA., Plioc. As., *Sansanosmilus* Mioc. Eu., Plioc. As., *Machairodus* Mioc.–Plioc. As., Mioc.–Pleist. Eu., Plioc. NA., Plioc.–Pleist. Af., *Metailurus* Mioc.–Plioc. As., *Homotherium* Plioc. Eu., ? *Aeluropsis Dinofelis* ?*Mellivorodon Propontosmilus Sivaelurus Sivasmilus* ?*Vinayakia Vishnufelis* Plioc. As., *Ischyrosmilus* Plioc. NA., *Epimachaerodus Paramachaerodus* Plioc. Eu. As., *Acinonyx* Plioc. Eu., R. As. Af., *Megantereon* Plioc.–Pleist. Eu. As., *Felis* [incl. *Panthera Lynx* etc.] Plioc.–R. Eu. As. NA., Pleist.–R. Af. SA., *Smilodon* Pleist. NA. SA.

INFRAORDER ARCTOIDEA. **F. Mustelidae**, R. Eu. As. Af. NA. SA., *Amphictis* Eoc.–Olig. Eu., *Plesictis* Eoc.–Mioc. Eu., *Mustelavus* Olig. NA., *Bunaelurus* Olig. NA. As., *Palaeogale* Olig.–Mioc. Eu., Mioc. As., *Aelurocyon Craterogale Megalictis Mephititaxus Mionictis Miomustela Oligobunis Paroligobunis Plionictis Promartes* Mioc. NA., *Ischyrictis Laphyctis Paralutra Pseudictis Trocharion Trochotherium* Mioc. Eu., *Potamotherium* Mioc. Eu., ?Mioc. NA., *Proputorius* Mioc. Eu., Plioc. As., *Brachypsalis Leptarctus Sthenictis* Mioc.–Plioc. NA., *Trochictis* Mioc.–Plioc. Eu., *Melodon* Mioc.–Plioc. As., *Mustela* Mioc.–R. NA. Eu., Plioc.–R. As., Pleist.–R. SA., R. Af., *Martes* ?Mioc., Plioc.–R. NA., Plioc.–R. Eu. As., *Canimartes Cernictis Lutravus Martinogale Pliogale Trigonictis* Plioc. NA., *Pannonictis Promeles Promephitis* Plioc. Eu., *Promellivora Vishnuonyx* Plioc. As., *Plesiogulo* Plioc. As. NA., *Parataxidea Sivaonyx Sivalictis* Plioc. Eu. As., *Eomellivora* Plioc. Eu. As NA., *Enhydriodon* Plioc. Eu. As. Af., *Sinictis* Plioc. Eu., Pleist. As., *Brachyprotoma* Plioc.–Pleist. NA., *Enhydrictis* Plioc.–Pleist. Eu. ?As., *Meles* Plioc.–R. Eu As., *Spilogale Taxidea* Plioc.–R. NA., *Lutra* Plioc.–R. Eu. As. NA., Pleist.–R. SA. Af., *Osmotherium Pelycictis* Pleist. NA., *Cyrnaonyx Nesolutra* Pleist. Eu., *Mellivora* Pleist. As., R. Af., *Arctonyx* Pleist.–R. As., *Aonyx* Pleist.–R. Af., *Conepatus Grison* [*Galictis*] Pleist.–R. NA. SA., *Mephitis* Pleist.–R. NA., *Lyncodon* Pleist.–R. SA., *Gulo* Pleist.–R. Eu. As. NA. **F. Canidae**, R. Eu. As. Af. NA. SA., *Procynodictis* Eoc. NA., *Amphicynodon* [*Cynodon*] *Paracynodon Plesiocyon Pseudamphicyon* Eoc.–Olig. Eu., *Cynodictis* Eoc –Olig. Eu. ?As., *Pachycynodon* Eoc.–Olig. Eu., Olig. As., *Amphicticeps* Olig. As., *Pseudocynodictis Brachyrhynchocyon* Olig. NA., *Daphoenus Mesocyon Nothocyon Parictis* Olig.–Mioc. NA., *Amphictis Haplocyon Pseudocyon* Olig.–Mioc. Eu., *Cephalogale* Olig.–Plioc. Eu., Mioc. As., *Amphicyon* Olig.–Plioc. Eu., Mioc.–Plioc. As. NA., Mioc. Af., *Allocyon Borocyon Daphoenodon Enhydrocyon Euplocyon Mammocyon Paradaphoenus Pericyon Philotrox Temnocyon Thaumastocyon* Mioc. NA., *Alopecocyon Amphi-*

cyonopsis Galecynus Haplocynoides Pseudarctos Tomocyon Mioc. Eu., *Gobicyon* Mioc. As., *Aelurodon Cynodesmus Ischyrocyon Osteoborus Pliocyon Tephrocyon Tomarctus* Mioc.–Plioc. NA., *Dinocyon* Mioc.–Plioc. Eu., *Areocyon Borophagus Hadrocyon Leptocyon Pliogulo* Plioc. NA., *Arctamphicyon Vishnucyon* Plioc. As., *Metarctos Simocyon* Plioc. Eu., *Hyaenognathus* Plioc.–Pleist. NA., *Canis* Plioc.–R. NA., Pleist.–R. Eu. As. Af. Aus. SA., *Theriodictis* Pleist. SA., *Nyctereutes Sivacyon* Pleist. As., *Protocyon* Pleist. Af., *Lycaon* Pleist.–R. Af., *Leucocyon* Pleist.–R. Eu., *Alopex* Pleist.–R. Eu. As., *Cuon* [*Cyon*] Pleist.–R. As., *Urocyon* Pleist.–R. NA., *Chrysocyon Dusicyon Paleocyon Speothos* [*Icticyon*] Pleist.–R. SA., *Vulpes* Pleist.–R. Eu. As. Af. NA. **F. Procyonidae,** R. NA. SA. EAs., *Aletocyon Bassariscops Cynarctoides Phlaocyon Zodiolestes* Mioc. NA., *Cynarctus* Mioc.–Plioc. NA., *Bassariscus* Mioc.–R. NA., *Sivanasua* Mioc. Eu., Plioc. As., *Parailurus* Plioc. Eu., *Cyonasua* Plioc. SA., *Procyon* Plioc.–R. NA., Pleist.–R. SA., *Brachynasua* Pleist. SA., *Nasua* Pleist.–R. SA., *Ailuropoda* [*Ailuropus*] Pleist.–R. As. **F. Ursidae,** R. Eu. As. NA. SA., *Hemicyon* Mioc. Eu. As. NA., *Ursavus* Mioc.–Plioc. Eu., *Indarctos* Plioc. Eu. As. NA., *Plionarctos* Plioc. NA., *Hyaenarctos* [*Agriotherium*] Plioc. Eu. NA., Plioc.–Pleist. As., *Holarctos* Plioc. Eu., Pleist.–R. As., *Ursus* Plioc.–R. Eu., Pleist. NAf., Pleist.–R. As. NA., *Arctodus Tremarctotherium* Pleist. NA., *Arctotherium Pararctotherium* Pleist. SA., *Melursus* Pleist.–R. As.

SUBORDER PINNIPEDIA. **F. Otariidae,** R. Pac., *Allodesmus Desmatophoca Dusignathus Neotherium Pithanotaria Pliopedia* Mioc. WNA., *Eumetopias* Mioc. Eu. EAs., Pleist. NA. SA., R. Pac., *Pontolis* Mioc.–Plioc. WNA., *Arctocephalus* Plioc. SA., Pleist. Aus. NZ., R. Pac., *Zalophus* Plioc. Aus., Pleist. WNA. NZ., R. Pac., *Otaria* Pleist. NA. SA., R. Pac. **F. Phocidae,** R. Oc., *Leptophoca* Mioc. NA., *Miophoca Monotherium Prophoca* Mioc. Eu., *Phoca* Mioc.–R. Eu. NA., Plioc.–R. As., *Callophoca Gryphoca Mesotaria Palaeophoca Phocanella Platyphoca Pristiphoca* Plioc. Eu., *Cystophora* Pleist.–R. NA. **F. Semantoridae,** *Semantor* Plioc. WAs. **F. Odobenidae,** R. Arc., *Prorosmarus* Mioc. NA., *Alachtherium* Plioc. Eu., *Odobenus* ["*Trichechus*"] Pleist. Eu. NA., R. Arc.

ORDER AMBLYPODA (PANTODONTA). **F. Coryphodontidae,** *Pantolambda Sparactolambda Titanoides* Paleoc. NA., *Coryphodon* Paleoc.–Eoc. NA., Eoc. Eu., *Eudinoceras* Eoc. As., *Hypercoryphodon* Olig. As. **F. Barylambdidae,** *Barylambda Haplolambda* Paleoc. NA. **F. Pantolambdodontidae,** *Pantolambdodon* Eoc. As.

ORDER DINOCERATA. **F. Uintatheriidae,** *Bathyopsoides* Paleoc. NA., *Prodinoceras* Paleoc. As., *Probathyopsis* Paleoc.–Eoc. NA., *Bathyopsis Elachoceras Eobasileus Uintatherium* [*Dinoceras*] Eoc. NA., *Gobiatherium* Eoc. As.

ORDER ASTRAPOTHERIA. **F. Trigonostylopidae,** *Shecenia* Paleoc. SA., *Scabellia Trigonostylops* Eoc. SA. **F. Astrapotheriidae,** *Albertogaudrya Astraponotus* Eoc. SA., *Astrapothericulus Parastrapotherium* Olig. SA., *Astrapotherium* Olig.–Mioc. SA., *Uruguaytherium Xenastrapotherium* Mioc. SA.

ORDER PYROTHERIA. **F. Pyrotheriidae,** ?*Carodnia* ?*Ctalecarodnia* Paleoc. SA., *Carolozittelia Propyrotherium* Eoc. SA., *Griphodon Pyrotherium* Olig. SA.

ORDER HYRACOIDEA. **F. Hyracidae (Procaviidae),** R. Af. WAs., *Pachyhyrax Saghatherium* Olig. Af., *Prohyrax* Mioc. Af., *Pliohyrax* Mioc. Af. Plioc. Eu., *Hyrax* [*Procavia*] Pleist.–R. Af., R. WAs. **Geniohyidae,** *Bunohyrax Geniohyus Megalohyrax Mixohyrax Titanohyrax* Olig. Af. **F. Myohyracidae,** *Myohyrax Protypotheroides* Mioc. Af.

ORDER EMBRITHOPODA. **F. Arsinoitheriidae,** *Arsinoitherium* Olig. Af.

ORDER PROBOSCIDEA

SUBORDER MOERITHERIOIDEA. **F. Moeritheriidae,** *Moeritherium* Eoc.–Olig. Af.

SUBORDER DINOTHERIOIDEA. **F. Dinotheriidae,** *Dinotherium* Mioc.–Plioc. Eu. As., Mioc.–Pleist. Af.

SUBORDER BARYTHERIOIDEA. **F. Barytheriidae,** *Barytherium* Eoc. Af.

SUBORDER ELEPHANTOIDEA. **F. Gomphotheriidae,** *Phiomia* Olig. Af., *Platybelodon* Mioc. As., Mioc.–Plioc. NA., *Gomphotherium* [*Trilophodon Bunolophodon Tetrabelodon*] Mioc. Af., Mioc.–Plioc. Eu. As. NA., *Serridentinus* Mioc. Eu., Mioc.–Plioc. As. NA., *Rhynchotherium* [*Dibelodon*] Mioc. Af., Mioc.–Pleist. NA., Plioc. As., *Synconolophus* Mioc.–Plioc. As., *Tetralophodon* Mioc.–Plioc. As. NA., Plioc. Eu., *Amebelodon Eubelodon Gnathobelodon* Plioc. NA., *Cuvieronius* [*Cordillerion*] Plioc. NA., Pleist. SA., *Anancus* Plioc.–Pleist. Eu. As., *Notiomastodon* Pleist. SA., *Stegomastodon* Pleist. NA. SA. **F. Mastodontidae,** *Palaeomastodon* Olig. Af., *Mastodon* Mioc.–Plioc. Eu., Mioc. Af., Mioc.–Pleist. NA., Plioc. As. **F. Elephantidae,** R. As. Af., *Stegolophodon* Plioc. Eu., Plioc.–Pleist. As., *Stegodon* Plioc.–Pleist. As., Pleist. Af., *Loxodonta* [*Palaeoloxodon,* etc.] Pleist. Eu. As., Pleist.–R. Af., *Mammuthus* [*Mammonteus Parelephas Archidiskodon*] Pleist. Eu. As. Af. NA., *Elephas* Pleist.–R. As.

ORDER SIRENIA

SUBORDER HALICORIFORMES. **F. Prorastomidae,** *Prorastomus* Paleoc. WInd., *Protosiren* Eoc. NAf. Eu. **F. Halicoridae (Dugongidae),** R. Ind.Oc. NPac., *Eotheroides* [*Eotherium Archaeosiren Eosiren*] Eoc. Af., *Prototherium* Eoc. Eu., *Manatherium Rytiodus* Olig. Eu., *Halitherium* Olig.–Mioc. Eu. NA. WInd., *Prohalicore Thalattosiren* Mioc. Eu., *Metaxytherium* [*Halianassa*] Mioc. Eu. NA., *Hesperosiren* Mioc. NA., *Felsinotherium* Plioc. Eu. NA., *Miosiren* Plioc. Eu., *Rytina* Subrecent NPac. **F. Manatidae (Trichechidae),** R. Atl., *Manatus* [*Trichechus*] Pleist.–R. NA. SA., R. Atl.

SUBORDER DESMOSTYLIFORMES. **F. Desmostylidae,** *Cornwallius* Olig. NA., *Desmostylus* Mioc. EAs. NA.

ORDER TUBULIDENTATA. **F. Orycteropodidae,** R. Af., ?*Tubulodon* Eoc. NA., ?*Palaeorycteropus* Eoc.–Olig. Eu., *Orycteropus* Plioc. Eu. As., Pleist.–R. Af., *Plesiorycteropus* Pleist. Mad.

ORDER CONDYLARTHRA. **F. Phenacodontidae,** *Desmatoclaenus Gidleyina Tetraclaenodon* [*Euprotogonia*] Paleoc. NA., *Ectocion* Paleoc.–Eoc. NA., *Phenacodus* Paleoc.–Eoc. NA., Eoc. Eu. **F. Hyopsodontidae,** *Choeroclaenus Dracoclaenus Ellipsodon Haplaletes Jepsenia Litaletes Litolestes Litomylus Mioclaenus Oxyacodon Oxytomodon Phenacodaptes Protoselene Tiznatzinia* Paleoc. NA., *Haplomylus* Paleoc.–Eoc. NA., *Hyopsodus* Eoc. NA. **F. Meniscotheriidae,** *Pleuraspidotherium Orthaspidotherium* Paleoc. Eu., *Meniscotherium* Paleoc.–Eoc. NA. **F. Didolodontidae,** *Ernestkokenia* [*Notoprotogonia*] Paleoc.–Eoc. SA., *Archaeohyracotherium Argyrolambda Asmithwoodwardia Didolodus Enneoconus Glyphodon Paulogervaisia Proectocion* Eoc. SA. **F. Periptychidae,** *Anisonchus Carsioptychius Conacodon ?Coriphagus Ectoconus Haploconus Hemithlaeus Mixoclaenus Periptychus Plagioptychus* Paleoc. NA. **Incertae sedis,** *Phenacolophus* Paleoc. As. *Tricuspiodon* Paleoc. Eu.

ORDER LITOPTERNA. **F. Proterotheriidae,** ?*Wainka* Paleoc. SA., *Guilielmofloweria* ?Paleoc., Eoc. SA., *Josepholeidya Ricardolydekkeria* Paleoc.–Eoc. SA., *Anisolambda Decaconus Megacrodon Polyacrodon Polymorphis* Eoc. SA., *Deuterotherium Eoproterotherium Paramacrauchenia Prolicaphrium Protheosodon Prothoatherium* Olig.

SA., *Licaprops* Olig.–Mioc. SA., *Licaphrium Thoatherium* Mioc. SA., *Brachytherium Diadiaphorus Proterotherium* Mioc.–Plioc. SA., *Chalpalmatherium Diplasiotherium Eoauchenia Epecuenia Trachypotherium* Plioc. SA. **F. Macraucheniidae,** *Victorlemoinea* Paleoc.-Eoc. SA., *Amilnedwardsia Ernestohaeckelia Lambdaconus Pseudadianthus Rutimeyeria* Eoc. SA., *Coniopternium Cramauchenia Notodiaphorus Proadianthus Prohepatoconus Tricoelodus* Olig. SA., *Theosodon* Olig.–Mioc. SA., *Adianthus Cullinia Oxyodontherium Paranauchenia Phoenixauchenia* Mioc. SA., *Scalibrinitherium* Mioc.–Plioc. SA., *Macrauchenidia Promacrauchenia Windhausenia* Plioc. SA., *Macrauchenia* Plioc.–Pleist. SA.

ORDER NOTOUNGULATA

SUBORDER NOTIOPROGONIA. **F. Arctostylopidae,** *Palaeostylops* Paleoc. As., *Arctostylops* Eoc. NA. **F. Henricosborniidae,** ?*Seudenius* Paleoc. SA., *Henricosbornia* Paleoc.–Eoc. SA., *Polystylops Postpithecus Peripantostylops* ?Paleoc., Eoc. SA., *Monolophodon Othnielmarshia* Eoc. SA. **F. Notostylopidae,** *Homalostylops Notostylops Otronia* Eoc. SA.

SUBORDER ENTYLONYCHIA. **F. Homalodotheriidae,** *Brandmayria* Paleoc. SA., *Isotemnus* [*Eochalicotherium*] ?Paleoc., Eoc. SA., *Calodontotherium Distylophorus Edvardotrouessartia Grypolophodon Lafkenia Periphragnis Pleurostylodon Rhyphodon Thomashuxleya* Eoc. SA., *Asmodeus Diorotherium Henricofilholia Lophocoelus Pleurocoelodon Prochalicotherium Trimerostephanos* Olig. SA., *Chasicotherium Homalodotherium* Mioc. SA.

SUBORDER TOXODONTIA. **F. Acoelodidae,** *Kibenikhoria* Paleoc. SA., *Acoelodus Maxschlosseria Oldfieldthomasia Paracoelodus Tsamnichoria Ultrapithecus* Eoc. SA. **F. Archaeopithecidae,** *Acropithecus Archaeopithecus* Eoc. SA. **F. Archaeohyracidae,** *Acoelohyrax Degonia Eohyrax* Eoc. SA., *Archaeohyrax* Olig. SA. **F. Leontiniidae,** *Ancylocoelus Colpodon Leontinia Scarrittia* Olig. SA. **F. Notohippidae,** *Eomorphippus Pseudostylops* Eoc. SA., *Interhippus* Eoc.–Olig. SA., *Argyrohippus Coresodon Eurygenium Morphippus Nesohippus Perhippidion Rhynchippus Stilhippus* Olig. SA., *Notohippus* Mioc. SA. **F. Toxodontidae,** *Proadinotherium Pronesodon* Olig. SA., *Adinotherium Eutomodus Gyrinodon Haplodontherium Nesodon Paratrigonodon Phobereotherium Prototrigodon Stenotephanos Stereotoxodon Eutrigonodon* Mioc. SA., *Toxodontherium* Mioc.–Plioc. SA., *Alitoxodon* Plioc. SA., *Toxodon Xotodon* Plioc.–Pleist. SA.

SUBORDER HEGETOTHERIA. **F. Hegetotheriidae,** *Eohegetotherium Eopachyrucos* Eoc. SA., *Prohegetotherium Propachyrucos Prosotherium* Olig. SA., *Hegetotherium* Olig.–Mioc. SA., *Pachyrukhos* Olig.–Plioc. SA., *Pseudohegetotherium* Mioc. ?Plioc. SA., *Hemihegetotherium Tremacyllus* Plioc. SA., *Paedotherium* Plioc.–Pleist. SA.

SUBORDER TYPOTHERIA. **F. Interatheriidae,** *Notopithecus* Paleoc.–Eoc. SA., *Transpithecus* ?Paleoc., Eoc. SA., *Guilielmoscottia* Eoc. SA., *Archaeophylus Cochilius Paracochilius Phanophilus Plagiarthrus Progaleopithecus* Olig. SA., *Protypotherium* Olig.–Plioc. SA., *Caenophilus Epipatriarchus Interatherium Munizia* Mioc. SA. **F. Typotheriidae** *Epitypotherium Isotypotherium* Eoc. SA., *Isoproedrium Proedium Trachytherus* Olig. SA., *Acrotypotherium Eutypotherium Typothericulus* Mioc. SA., *Pseudotypotherium Typotheriopsis Xenotherium* Plioc. SA., *Typotheriodon Typotherium* [*Mesotherium*] Plioc.–Pleist. SA., *Bravardia* Pleist. SA.

ORDER PERISSODACTYLA

SUBORDER HIPPOMORPHA

SUPERFAMILY EQUOIDEA. **F. Equidae,** R. As. Af., *Hyracotherium* Eoc. Eu., *Eohippus* Eoc. NA., *Epihippus Orohippus* Eoc. NA., *Mesohippus* Olig. NA., *Miohippus*

Olig.–Mioc. NA., *Anchitherium* Mioc. As. NA. Eu., *Archaeohippus Parahippus* Mioc. NA., *Hypohippus* Mioc.–Plioc. NA., Plioc. As., *Merychippus* [*Protohippus*] *Pliohippus* Mioc.–Plioc. NA., *Calippus Megahippus Nannippus Neohipparion* Plioc. NA., *Hipparion* Plioc. NA. Eu. As., Plioc.–Pleist. Af., *Hippidion Hyperhippidium Onohippidium* Pleist. SA., *Equus* [*Asinus Hemionus Hippotigris Neohippus Plesippus*] Pleist. Eu. NA. SA., Pleist.–R. Af. As. F. **Palaeotheriidae,** *Anchilophus Lophiotherium Pachynolophus Plagiolophus Propachynolophus* Eoc. Eu., *Propalaeotherium* Eoc. Eu. As., *Palaeotherium Paloplotherium* Eoc.–Olig. Eu.

SUPERFAMILY TITANOTHERIOIDEA. F. **Chalicotheriidae,** *Eomoropus* Eoc. NA. EAs., *Grangeria* Eoc.–Olig. As., *Oreinotherium* Olig. NA., *Pernatherium* Olig. Eu., *Schizotherium* Olig. Eu. As., *Metaschizotherium* Mioc. Eu., *Moropus* Mioc. NA., *Phylotillon* Mioc. As., *Macrotherium* Mioc. Af., Mioc.–Plioc. Eu. As. NA., *Chalicotherium* Plioc. Eu., *Ancylotherium* Plioc. Eu. WAs., ?Pleist. Af., *Nestoritherium* [*Circotherium*] *Postschizotherium* Pleist. As. F. **Titanotheriidae,** *Diplacodon Dolichorhinus Eometarhinus Eotitanops Eotitanotherium Lambdotherium Limnohyops Manteoceras Mesatirhinus Metarhinus Notiotitanops Palaeosyops Protitanotherium Rhadinorhinus Sphenocoelus Sthenodectes Telmatherium* Eoc. NA., *Teleodus* Eoc.–Olig. NA., *Brachydiastematherium* Eoc. Eu., *Metatalmatherium* Eoc. As. NA., *Desmatotitan Dolichorhinoides Epimanteoceras Gnathotitan Microtitan Pachytitan Protitan Rhinotitan Sivatitanops Titanodectes* Eoc. As., *Embolotherium Hyotitan Parabrontops Metatitan* Olig. As., *Brontops Brontotherium Megacerops Titanotherium* [*Menodus*] *Protitanops* Olig. NA.

SUBORDER TAPIROMORPHA

SUPERFAMILY TAPIROIDEA. F. **Helaletidae (Colodontidae),** *Dilophodon Helaletes Heptodon Heteraletes* Eoc. NA., *Desmatotherium* Eoc. NA. As., *Deperetella Diplolophodon ?Lophialetes ?Schlosseria Telelophus* Eoc. As., *Paracolodon* Olig. As., *Colodon* Olig. NA. As. F. **Lophiodontidae,** *?Chasmotheroides* Eoc. NA., *Cristidentinus* Eoc. As., *Atalonodon Chasmotherium Lophiaspis Lophiodon Lophiodochoerus* Eoc. Eu. F. **Isectolophidae,** *Indolophus* Eoc. As., *Homogalax* [*Systemodon*] *Parisectolophus Schizolophodon* Eoc. NA. F. **Tapiridae,** R. CA. SA. SAs., *Protapirus* Olig. Eu., Olig.–Mioc. NA., *Paratapirus* Mioc. As., *Palaeotapirus* Mioc. Eu., *Miotapirus Tapiravus* Mioc. NA., *Tapirus* Plioc.–Pleist. Eu., Plioc.–R. As., Pleist. NA., Pleist.–R. SA., R. CA., *Megatapirus* Pleist. As.

SUPERFAMILY RHINOCEROTOIDEA. F. **Hyrachyidae,** *Colonoceras Ephyrachyus Hyrachyus Metahyrachyus* Eoc. NA. F. **Hyracodontidae** *Ardynia Caenolophus Teilhardia* Eoc. As., *Epitriplopus Prothyracodon Triplopus* Eoc. NA., *Hyracodon* Olig. NA. F. **Amynodontidae,** *Amynodontopsis Mesamynodon* Eoc. NA., *Amynodon* Eoc. NA. As., *Paramynodon* Eoc. As., *Metamynodon* Olig. NA. As., *Cadurcotherium* Olig. Eu. Mioc. As. F. **Rhinocerotidae,** R. SAs. EInd. Af., *Eotrigonias* Eoc. NA., *Prohyracodon* Eoc. Eu., *Forstercooperia* Eoc. As., *Amphicaenops Caenopus Subhyracodon Trigonias* Olig. NA., *Allocerops Eggysodon Epiaceratherium Meninatherium Preaceratherium Protaceratherium Ronzotherium* Olig. Eu., *Indricotherium Paraceratherium* Olig. As., *Aceratherium* Olig.–Mioc. Eu., Mioc. Af., Mioc.–Plioc. As., *Baluchitherium* Olig.–Mioc. As., *Pleuroceros* Olig.–Mioc. Eu., Mioc. As., *Brachypotherium* Mioc. Eu. ?Af., *Diceratherium* [*Menoceras Metacaenopus*] Mioc. NA., *Plesiaceratherium* Mioc. As., *Dicerorhinus* [*Ceratorhinus*] Mioc.–Pleist. Eu., Mioc.–R. SAs., Pleist.–R. Eu., *Aphelops Peraceras Teleoceras* Mioc.–Plioc. NA., *Chilotherium* Mioc.–Plioc. As. Eu., *Gaindatherium Iranotherium Sinotherium* Plioc. As., *Diceros* [*Atelodus Opsiceros*] Plioc. Eu., Pleist.–R.

Af., *Ceratotherium* Pleist.–R. Af., *Coelodonta* [*Tichorhinus*] Pleist. As. Eu., *Elasmotherium* Pleist. Eu. NAs., *Rhinoceros* Pleist.–R. As. EInd.

ORDER ARTIODACTYLA

SUBORDER PALAEODONTA. **F. Homacodontidae,** *Bunomeryx Diacodexis Homacodon Hylomeryx Mesomeryx ?Microsus Pentacemylus ?Sarcolemur Sphenomeryx Wasatchia* Eoc. NA. **F. Leptochoeridae,** *Leptochoerus Stibarus* Olig. NA. **F. Dichobunidae,** *Meriscodon Protodichobune* Eoc. Eu., *Dichobune Mouillacitherium* Eoc.–Olig. Eu., *Hyperdichobune* Olig. Eu.

SUBORDER SUINA. **F. Choeropotamidae,** *Bunophorus Helohyus ?Lophiohyus Parahyus* Eoc. NA., *Gobiohyus* Eoc. As., *Choeropotamus* Eoc.–Olig. Eu. **F. Entelodontidae,** *Entelodon* [*Elotherium*] Olig. Eu., *Archaeotherium Megachoerus Pelonax Scaptohyus* Olig. NA., *Boöchoerus Choerodon Daeodon Dinohyus* Mioc. NA., *?Bugtitherium* Mioc. As., *?Tetraconodon* Plioc.–Pleist. As. **F. Achaenodontidae,** *Achaenodon* Eoc. NA. **F. Cebochoeridae,** *Brachyhyops* Eoc. NA., *Cebochoerus Mixtotherium* Eoc. Eu., *Choeromorus* ?Eoc. EInd., Eoc.–Olig. Eu. **F. Suidae,** R. As. Af. EInd., *Propalaeochoerus* Olig. Eu., Mioc. Af., *Hyotherium Mesochoerus Xenochoerus* Mioc. Eu., *Diamantohyus* Mioc. Af., *Listriodon* Mioc. Eu. Af., Mioc.–Plioc. As., *Palaeochoerus* Mioc. Eu., Mioc.–Plioc. As., *Chleuastochoerus Conohyus Hyosus Lophochoerus Propotamochoerus Sanitherium Sivahyus* Plioc. As., *Microstonyx* Plioc. Eu., *Potamochoerus* Plioc. Eu., Pleist. As., Pleist.–R. Af., *Sivachoerus* Plioc. NAf., Plioc.–Pleist. As., *Dicoryphochoerus Hippohyus* Plioc.–Pleist. As., *Phacochoerus* Plioc.–R. Af., Pleist. WAs., *Sus* Plioc.–R. Eu. Af. As., Pleist.–R. EInd., *Kolpochoerus Notochoerus* [*Metridiochoerus*] Pleist. Af., *Koiropotamus Hylochoerus* Pleist.–R. Af. **F. Dicotylidae (Tayassuidae),** R. CA. SA., *Doliochoerus* Olig. Eu., *Perchoerus* [*Thinohyus*] Olig.–Mioc. NA., *Chaenohyus Desmathyus Dyseohyus Floridachoerus Hesperhys Pediohyus* Mioc. NA., *Choerotherium* Mioc. Eu., *Prosthenops* Mioc.–Plioc. NA., ?Pleist. SA., *Pecarichoerus* Plioc. As., *Platygonus* Plioc.–Pleist. NA., Pleist. SA., *Mylohyus* Pleist. NA. ?SA., *Catagonus Leptotherium* Pleist. SA., *Dicotyles* [*Tayassu Tagassu*] Pleist.–R. NA. SA. **F. Anthracotheriidae,** *Anthracobune Anthracohyus Anthracokeryx Anthracosenex Anthracothema* Eoc. As., *Haplobunodon Lophiobunodon Thaumastognathus* Eoc. Eu., *Rhagatherium* Eoc.–Olig. Eu., Olig. Af., ?Plioc. As., *Gelasmodon* Olig. As., *Brachyodus* Olig. As., Olig.–Mioc. Eu. Af., *Bothriogenys* Olig. Af., *Elomeryx Heptacodon Octacodon* Olig. NA., *Bunobrachyodus* Olig. Eu., *Bothriodon* [*Ancodus Hyopotamus*] Olig. Eu. NA., Olig.–Mioc. Af., *Microbunodon* [*Microselenodon*] Olig. Eu., Plioc. As., *Anthracotherium* Olig. Eu., Mioc.–Plioc. As., *Arretotherium* Mioc. NA., *Parabrachyodus* Mioc. As., *Hyoboöps* Mioc. Af., Mioc.–Plioc. As., *Hemimeryx Telmatodon* Mioc.–Plioc. As., *Choeromeryx* Plioc. As., *Merycopotamus* Plioc. NAf., Plioc.–Pleist. As., Pleist. EInd. **F. Hippopotamidae,** R. Af., *Hippopotamus* [*Hexaprotodon Choeropsis*] Plioc.–Pleist. As., Plioc.–R. Af., Pleist. Eu. EInd.

SUBORDER RUMINANTIA

INFRAORDER TYLOPODA. **F. Caenotheriidae,** *Oxacron Paroxacron* Eoc.–Olig. Eu., *Caenomeryx Plesiomeryx Procaenotherium* Olig. Eu., *Caenotherium* Olig.–Mioc. Eu. **F. Anoplotheriidae,** *Catodontherium Dacrytherium Leptotheridium* Eoc. Eu., *Anoplotherium Diplobune Tapirulus* Eoc.–Olig. Eu., *Ephelcomenus* [*Hyracodontherium*] Olig. Eu. **F. Xiphodontidae,** *Haplomeryx Xiphodon* Eoc. Eu., *Dichodon* [*Tetraselenodon*] Eoc.–Olig. Eu. **F. Camelidae,** R. As. Af. SA., *?Camelodon Poabromylus Protylopus* Eoc. NA., *Dyseotylopus Eotylopus Poëbrotherium Pseudolabis* Olig. NA., *Paratylopus Protomeryx* Olig.–Mioc. NA., *Gentilicamelus Miolabis Miotyl-*

opus Oxydactylus Stenomylus Mioc. NA., *Alticamelus Procamelus Protolabis* Mioc.–Plioc. NA., *Megacamelus Megatylopus Pliauchenia Pseudoceras Rakomylus* Plioc. NA., *Camelops Gigantocamelus Tanupolama Titanotylopus* Pleist. NA., *Camelus* Pleist. Eu. ?NA., Pleist.–R. Af. As., *Paleolama* [*Hemiauchenia*] *Protauchenia* Pleist. SA., *Paracamelus* Pleist. Eu. As., *Auchenia* [*Lama Vicugna*] Pleist.–R. SA. **F. Oreodontidae (Merycoidodontidae),** *Hyomeryx Protoreodon* [*Eomeryx*] Eoc. NA., *Bathygenys Eucrotaphus Limnenetes Oreodon* [*Merycoidodon*] *Oreonetes* Olig. NA., *Eporeodon Leptauchenia* Olig.–Mioc. NA., *Cyclopidius* [*Brachymeryx Pithecistes Sespia*] *Mediochoerus Merychyus Merycochoerus Merycoides Mesoreodon Oreodontoides Paroreodon Phenacocoelus Poatrephes Promerycochoerus*, *Pronomotherium* [*Brachycrus Chelonocephalus*] *Ticholeptus* Mioc. NA., *Metoreodon* Mioc.–Plioc. NA., *Ustatochoerus* Plioc. NA. **F. Agriochoeridae,** *Diplobunops Mesagriochoerus Protagriochoerus* Eoc. NA., *Agriochoerus* Olig.–Mioc. NA.

INFRAORDER PECORA

SUPERFAMILY TRAGULOIDEA. **F. Amphimerycidae,** *Amphimeryx Pseudamphimeryx* Eoc.–Olig. Eu. **F. Hypertragulidae,** *Camelomeryx Leptoreodon* [*Hesperomeryx*] *Leptotragulus Oromeryx Simimeryx* Eoc. NA., *Archaeomeryx* Eoc. As., *Heteromeryx Hypisodus* Olig. NA., *Hypertragulus Leptomeryx Nanotragulus* Olig.–Mioc. NA., *Allomeryx Floridatragulus Hypermekops* Mioc. NA. **F. Protoceratidae,** *Calops Protoceras* Olig. NA., *Syndyoceras* Mioc. NA., *Paratoceras Synthetoceras* [*Prosynthetoceras*] Plioc. NA. **F. Tragulidae,** *Indomeryx* Eoc. As., *Phaneromeryx* Eoc. Eu., *Cryptomeryx Gelocus* Eoc.–Olig. Eu., *Lophiomeryx* Olig. Eu. As., *Eumeryx Miomeryx* Olig. As., *Paragelocus Pseudogelocus* Olig. Eu., *Bachitherium Prodremotherium* Olig. Eu., ?Mioc. Af., *Dorcatherium* Mioc. Af., Mioc.–Plioc. Eu. As., *Dorcabune* Plioc. As., *Tragulus* Plioc.–R. As., *Hyemoschus* Pleist.–R. Af.

SUPERFAMILY CERVOIDEA. **F. Palaeomerycidae,** *Aletomeryx Barbourmeryx Blastomeryx Bouromeryx Drepanomeryx Dromomeryx Dyseomeryx Machaeromeryx Matthomeryx Parablastomeryx Rakomeryx* Mioc. NA., *Climacocerus* Mioc. Af., *Procervulus* Mioc. Eu., *Amphitragulus* Mioc. Eu. As. Af., *Dremotherium* Olig.–Mioc. Eu., Mioc. As., *Palaeomeryx* Mioc. Eu. As., *Lagomeryx* [*Heterocemas*] Mioc. Eu., Mioc.–Plioc. As., *Cranioceras Longirostromeryx* Mioc.–Plioc. NA., *?Pediomeryx* Plioc. NA. *?Moschus* Plioc.–R. As., **F. Cervidae,** R. Eu. As. NA. SA., *Palaeoplatycerus* Mioc. Eu., *Stephanocemas* Mioc. Eu. As., *Micromeryx* Mioc. Eu., Plioc. As., *Dicrocerus* [*Heteroprox Euprox*] Mioc.–Plioc. Eu. As., *Cervavitus Euctenoceros Metacervocerus Pliocervus Procerus* Plioc. Eu., *Bohlinella* ?Plioc. EAs., *Cervavus Eostyloceros Epirusa Paracervulus Platycemas* Plioc. As., *Cervocerus Procapreolus* Plioc. Eu. As., *Metacervulus* Plioc. Eu., Plioc.–Pleist. As., *Axis* Plioc.–Pleist. Eu., Pleist. EInd., Pleist.–R. As., *Eucladoceros* [*Polycladus*] Plioc.–Pleist. Eu. As., *Elaphurus Pseudaxis* Plioc.–R. As., *Muntiacus* [*Cervulus*] Plioc.–R. As., Pleist. EInd., *Capreolus* Plioc.–R. Eu., Pleist.–R. As., *Cervus* [*Elaphus Euryceros*] Plioc.–R. Eu. As., Pleist. NAf., Pleist.–R. NA., *Cervalces Procoileus* Pleist. NA., *Antifer* [*Paraceras Habromeryx*] *Morenelaphus Palaeoödocoileus* Pleist. SA., *Megaceros* [*Alce*] Pleist. Eu., *Euryceros* Pleist. Eu. As. NAf., *Megaceroides* Pleist. NAf., *Sinomegaceros* Pleist. As., *Dama* Pleist. WAs., Pleist.–R. Eu. As., *Alces Rangifer* Pleist.–R. Eu. As. NA., *Odocoileus* Pleist.–R. NA. SA., *Hippocamelus Mazama Ozotoceros Pudu* [*Furcifer*] Pleist.–R. SA., *Hydropotes Rucervus Rusa* Pleist.–R. As. **F. Giraffidae,** R. Af., *Palaeotragus* [*Achtiaria*] Mioc.–Plioc. As. Eu., *?Propalaeomeryx* [*Progiraffa*] Mioc.–Plioc. As., *Bramatherium Giraffokeryx Honanotherium Hydaspidotherium Vishnutherium* Plioc. As., *Samotherium* Plioc. Eu. As., *?Libytherium* Plioc. Af., *Bohlinia* [*Orasius*] Plioc. Eu., *Helladotherium*

[*Panotherium*] Plioc. Eu. WAs., Pleist. Af., *Giraffa* [*Camelopardalis*] Plioc.–Pleist. As., Pleist.–R. Af., *Griquatherium* Pleist. Af., *Sivatherium* [*Indratherium*] Pleist. As. Af.

SUPERFAMILY BOVOIDEA. **F. Antilocapridae,** R. NA., *Merycodus* [*Cosoryx*] *Ramoceros* [*Merriamoceros Paramoceros*] Mioc.–Plioc. NA., *Ceratomeryx Hexameryx Hexobelomeryx Meryceros* [*Submeryceros*] *Osbornoceros Proantilocapra Sphenophalos* [*Plioceros*] Plioc. NA., *Capromeryx* [*Dorcameryx Texoceros*] *Ilingoceros* Plioc.–Pleist. NA., *Tetrameryx* [*Hayoceros Stockoceros*] Pleist. NA., *Antilocapra* Pleist.–R. NA. **F. Bovidae,** R. Eu. As. EInd. Af. NA., *Eotragus* [*Eocerus*] *Strogulognathus* Mioc. Eu. Af., *Miotragoceros Protragocerus* Mioc. Eu., *Strepsiportax* ?Mioc. Eu., Plioc. As., *Protetraceros* Mioc. EAs., *Propalaeoryx* Mioc. Af., *Antilospira Cambayella Dorcadoryx Dorcadoxa Helicoportax Hydaspicobus Kobikeryx Lyrocerus Megalovis Olonbulukia Pachygazella Pachyportax Perimia Plesiaddax Proamphibos Proleptobos Prosinotragus Pseudobos Qurliqnoria Ruticeros Selenoportax Sinoreas Sinoryx Sinotragus Sivaceros Sivaportax Sivoreas Tossunnoria Tragoportax Tsaidamotherium Urmiatherium Vishnumeryx* Plioc. As., *Leptotragus Pachytragus Prodamaliscus Pseudotragus Samotragus* Plioc. WAs., *Criotherium Graecoryx Microtragus Parurmiatherium Prostrepsiceros* Plioc. WAs. Eu., *Helicoceras Helicophora Helicotragus Oioceros Palaeoryx Paraboselaphus Paraprotoryx Protoryx Protragelaphus Tragocerus Tragoreas* Plioc. As. Eu., *Gazellospira* Plioc. ?As., Eu., *Hemistrepsiceros Procamptoceras Procobus* Plioc. Eu., *Palaeoreas* Plioc. As., NAf., Plioc.–Pleist. Eu., *Connochaetes* ?Plioc. Eu., Pleist.–R. Af., *Sphenophalos* Plioc. NA., *Gazella* Plioc.–Pleist. Eu., Plioc.–R. As., Pleist.–R. Af., *Hippotragus* Plioc. Eu., Plioc.–Pleist. As., Pleist.–R. Af., *Nemorhaedus* Plioc. Eu., R. As., *Parabos* Plioc. Eu. Af., ?Pleist. NA., *Indoredunca Sivatragus* ?Plioc., Pleist. As., *Oreas Strepsiceros* Plioc. As., Pleist.–R. Af., *Hemibos Spirocerus* Plioc.–Pleist. As., *Taurotragus* Plioc.–Pleist. As., Pleist.–R. Af., *Boselaphus* Plioc.–R. As., *Antilope* Plioc.–R. As., Pleist. EInd., *Ovis* Plioc.–R. As., Pleist.–R. Eu. Af. NA., *Leptobos* Pleist. Eu. As. EInd., *Amphibos Boöpsis Bucapra Damalops Gangicobus Platybos Proboselaphus Probubalus Sivacapra Sivacobus Sivadenota Sivoryx Vishnucobus* Pleist. As., *Bularchus Megalotragus Orangiatherium Palaeotragiscus Parmularias Pelorovis Pelorocerus Phenacotragus Pultiphagonides Rhynotragus Thaleroceros* Pleist. Af., *Bathyleptodon* Pleist. EAf., *Aftonius Bootherium Euceratherium Gidleya Neotragocerus Preptoceras Symbos* Pleist. NA., ? *Nothobos* Pleist. SA., *Duboisia* Pleist. EInd., *Myotragus* Pleist. Balearic Is., *Poephagus* Pleist. Alaska, R. As., *Saiga* Pleist. Alaska, Pleist.–R. Eu. As., *Bison* [*Superbison Simobison Stelabison*] Pleist. As., Pleist.–R. Eu. NA., *Cobus* Pleist. As., Pleist.–R. Af., *Parabubalis* ?Pleist. As., *Hemitragus* Pleist. Eu., R. As., *Ovibos* Pleist. Eu. As., Pleist.–R. NA., *Antidorcas* Pleist. Eu. As., R. Af., *Bibos* Pleist. Eu., Pleist.–R. As. EInd., *Budorcas Pantholops Procapra Tetraceros* Pleist.–R. As., *Bubalus* Pleist.–R. As. EInd., *Bos Capra* Pleist.–R. As. Eu. NAf., *Ibex* Pleist.–R. Eu., *Rupicapra* Pleist.–R. Eu., R. WAs., *Addax Adenota Alcelaphus* [*Bubalis*] *Ammotragus Beatragus Cephalophus Cervicapra Damaliscus Gorgon Nesotragus Philantomba Redunca Sylvicapra Syncerus* Pleist.–R. Af., *Oryx* Pleist.–R. Af., R. WAs., *Oreamnos* Pleist.–R. NA.

ORDER EDENTATA (XENARTHRA)

SUBORDER PALAEANODONTA. **F. Metacheiromyidae,** *Palaeanodon* Paleoc.–Eoc. NA., *Metacheiromys* Eoc. NA. **F. Epoicotheriidae** *Epoicotherium Xenocranium* Olig. NA.

SUBORDER PILOSA

INFRAORDER GRAVIGRADA. **F. Megalonychidae,** *Orophodon Proschismotherium* Olig. SA., *Hapalops* Olig.–Mioc. SA., *Analcimorphus Eucholoeops Hyperleptus Mega-*

lonychotherium Menilaus Neohapalops Orthotherium Parahapalops Pelecyodon Pliomorphus Protomegalonyx Pseudohapalops Schismotherium Xyophorus Zamicrus Mioc. SA., *Pronothrotherium* Mioc.–Plioc. SA., ?Plioc. NA., ? *Amphiocnus Diheterocnus Heterocnus Megalonychotherium ?Sinclairia Synhapalops* Plioc. SA., *Megalonyx* Plioc.–Pleist. NA., *Nothrotherium* Pleist. NA. SA., *Nothropus* Pleist. SA., *Acratocnus Megalocnus Mesocnus Microcnus Miocnus Parocnus* Pleist. WInd. F. **Megatheriidae,** *Eomegatherium Megathericulus Planops Prepotherium* Mioc. SA., *Plesiomegatherium Promegatherium* Mioc.–Plioc. SA., *Megatherium* Mioc.–Pleist. SA., Pleist. NA., *Megatheridium Megatheriops Pliomegatherium Pyramiodontherium* Plioc. SA., *Neoracanthus Paramegatherium* Pleist. SA. **F. Mylodontidae,** *Octodontotherium* Olig. SA., *Analcitherium Diodomus Inthodon Nematherium Neonematherium Nephotherium Promylodon Ranculus Stenodontherium Strabosodon* Mioc. SA., *Scelidotherium* Mioc.–Pleist. SA., *Elassotherium Eumylodon Laniodon Octomylodon Pleurolestodon Proscelidodon Sphenotherus* Plioc. SA., *Glossotherium Lestodon Scelidodon* Plioc.–Pleist. SA., *Catonyx Paramylodon Platyonyx* Pleist. SA., *Mylodon* [*Neomylodon Grypotherium*] Pleist. SA. NA.

INFRAORDER TARDIGRADA. **F. Bradypodidae,** R. SA.

INFRAORDER VERMILINGUA. **F. Myrmecophagidae,** R. SA., ?*Promyrmecophagus* ?*Protamandua* Mioc. SA., *Neotamandua Palaeomyrmedon* Plioc. SA., *Myrmecophaga Tamandua* Pleist.–R. SA.

SUBORDER LORICATA. **F. Dasypodidae,** R. SA. CA., *Utaetus* Paleoc.–Eoc. SA., *Anteutatus Anutaetus Archeutatus Astegotherium Coelutaetus Hemieutatus Iseutatus Orthutaetus Pachyzaedius Posteutatus Pseudeutatus* Eoc. SA., *Meteutatus* Eoc.–Olig. SA., *Amblytatus Machlydotherium Pseudostegotherium Sadypus Stegotheriopsis* Olig. SA., *Prodasypus Proeutatus Prozaedius Stenotatus* Olig.–Mioc. SA., *Dasyprodon Pareutatus Praeeuphractus Stegotherium Vetelia* Mioc. SA., *Eutatus* Mioc.–Plioc. SA., *Acantharodeia Chaetophractus Doellotatus Eutatopsis Kraglievichia Macroeuphractus Plaina Pontotatus Proeuphractus Vasallia* Plioc. SA., *Chlamydotherium Propraopus* Plioc.–Pleist. SA., *Zaedyus* Plioc.–R. SA., *Dasypus* [*Tatu*] Plioc.–R. SA. NA., *Chlamydophorus* Pleist. SA., *Holmesina* Pleist. NA., *Euphractus Tolypeutes Xenurus* Pleist.–R. SA. **F. Peltephilidae,** *Parapeltocoelus* Olig. SA., *Peltecoelus Peltephilus* Olig.–Mioc. SA., *Anantiosodon Epipeltephilus* Mioc. SA. **F. Glyptodontidae,** *Glyptatelus Palaeopeltis* Eoc.–Olig. SA., *Lomaphorelus* Olig. SA., *Propalaehoplophorus* Olig.–Mioc. SA., *Asterostemma Chlamyphractus Cochlops Comaphorus Eucinepeltus Lomaphorops Metopotoxus Protoglyptodon Pseudoeuryurus* Mioc. SA., *Palaehoplophorus Parahoplophorus Urotherium* Mioc.–Plioc. SA., *Aspidocalyptus Berthawyleria Castellanoisia Coscinocercus Eleutherocercus Eosclerocalyptus Hoplophractus Nopachthus Palaeodaedicurus Paraglyptodon Plaxhaplus Plohophoroides Plohophorops Plohophorus Prodaedicurus Propanochthus Pseudoplohophorus Stromaphorus Stromaphoropsis Teisseiria Trabalia Trachycalyptus* Plioc. SA., *Daedicurus Glyptodon Lomaphorus Neuryurus Sclerocalyptus Xiphuroides* Plioc.–Pleist. SA., *Boreostracon Brachyostracon Euryodon Glyptotherium Heterodon Hoplophorus Neothoracophorus Panochthus Zaphilus* Pleist. SA.

Order Pholidota. **F. Manidae,** R. Af. SAs., ?*Leptomanis* Olig. Eu., ?*Galliaetatus* ?*Teutomanis* Mioc. Eu., *Manis* Pleist.–R. As., R. Af.

Order Cetacea

SUBORDER ARCHAEOCETI. **F. Protocetidae,** *Eocetus Pappocetus Prozeuglodon* Eoc. Af., *Protocetus* Eoc. Af. NA. **F. Dorudontidae,** *Dorudon* Eoc. Af. NA., *Zygrorhiza* Eoc. Eu. NA., *Kekenodon* Olig. NZ., *Phococetus* Mioc. Eu. **F. Basilosauridae** (Zeuglo-

dontidae), *Basilosaurus* [*Zeuglodon*] *?Pontogeneus* Eoc. NA., *Mammalodon* ?Eoc. Aus., *Pachycetus Platyosphys* Olig. Eu.

SUBORDER INCERTAE SEDIS. *Agriocetus Patriocetus* Olig. Eu.

SUBORDER ODONTOCETI. **F. Agorophiidae,** *Agorophius Archaeodelphis Xenorophus* Eoc. NA. **F. Squalodontidae,** *Microcetus* Olig. Eu. NZ., *Microzeuglodon* Olig.–Mioc. Eu., *Microsqualodon Neosqualodon Rhytisodon Trirhizodon* Mioc. Eu., *Squalodon* Mioc. Eu. NA. NZ., *Colophonodon Saurocetus* Mioc. NA., *Phoberodon* Mioc. SA., *Prosqualodon* Mioc. SA. Aus. ?NZ., *Tangarasaurus* Mioc. NZ., *Metasqualodon Parasqualodon Prionodelphis* Plioc. SA. **F. Iniidae,** R. SA. EAs., *Hesperocetus* Mioc. NA., *Proinia* Mioc. SA., *Anisodelphis Ischyrorhynchus Plicodontinia Pontoplanodes* [*Saurodelphis*] Plioc. SA., *Goniodelphis* Mioc.–Plioc. NA. **F. Ziphiidae,** R. Oc., *Anoplanassa Belemnoziphius Eboroziphius ?Pelycorhamphus Proroziphius* Mioc. NA., *Choneziphius* Mioc. NA., Mioc.–Plioc. Eu., *Mesoplodon* Mioc. NA., Mioc.–Plioc. Eu., R. Oc., *Incacetus Diochotichus* Mioc. SA., *Cetorhynchus Palaeoziphius Squalodelphis Ziphioides Ziphirostrum* [*Mioziphius*] Mioc. Eu., *Berardiopsis* Plioc. Eu. **F. Delphinidae,** R. Oc. SA., *Agabelus Allodelphis Belosphys Ceterhinops Delphinavus Delphinodon Doliodelphis Grypolithax Ixacanthus Kentriodon Lamprolithax Liolithax Lophocetus Loxolithax Macrodelphinus Megalodelphis Nannolithax Oedolithax Platylithax Priscodelphinus Tretosphys* Mioc. NA., *Champsodelphis Delphinopsis Eoplatanista Heterodelphis Iniopsis Macrochirifer Palaeophocaena Pithanodelphis Protodelphinus Protophocaena Stereodelphis Zyphiodelphis* Mioc. Eu., *Acrodelphis Pomatodelphis* Mioc. Eu. NA., *Argyrocetus* Mioc. NA. SA., *Eurhinodelphis* Mioc. Eu. NA. EAs., *Sinanodelphis* Mioc. EAs., *Schizodelphis* [*Cystodelphis*] Mioc. Af., Mioc. Eu. NA., *Miodelphis* Mioc. NA., Plioc. Eu., *Tursiops* ?Mioc., Plioc.–Pleist. Eu., Pleist. NA., R. Oc., *Lonchodelphis* Plioc. NA., *Pontistes Pontivaga* Plioc. SA., *Hemisyntrachelus Steno* Plioc. Eu., *Delphinus* Plioc. Eu., R. Oc., *Orcinus* [*Orca*] Plioc. EAs., Plioc.–Pleist. Eu., R. Oc., *Pseudorca* Plioc. Eu. EAs., R. Oc., *Delphinapterus* Pleist. Eu. NA., R. Oc., *Globicephala* Pleist. NA., R. Oc., *Stenodelphis* Pleist. NA., R. SA., *Phocaenopsis* Pleist. NZ., *Phocaena* Pleist. EAs., R. Oc., *Monodon* Pleist. Eu. NA., R. Arc. **F. Platanistidae,** R. SAs., *Zarhachis* Mioc. NA. **F. Kogiidae,** R. Oc., *Kogia* Plioc. EAs., R. Oc., *Kogiopsis* Plioc. NA. **F. Physeteridae,** R. Oc., *Aulophyseter Dinoziphius ?Graphiodon Idiophyseter Orycterocetus* Mioc. NA., *Ontocetus* Mioc. NA. EAs., *Diaphorocetus Idiorophus* Mioc. SA., *Scaptodon* Mioc. Aus., *Hoplocetus* Mioc. Eu. ?NA., *Physeterula Placoziphius Prophyseter Scaldicetus Thalassocetus* Mioc. Eu., *Physeter* Mioc.–Pleist. NA., Pleist. Eu., R. Oc., *Balaenodon Priscophyseter* Plioc. Eu., *Physetodon* Plioc. Aus.

SUBORDER MYSTICETI. **F. Cetotheriidae,** *Mauicetus* Olig. NZ., *Cephalotropis Cophocetus Mixocetus Parietobalaena Peripolocetus Rhagnopsis Siphonocetus Tiphyocetus Tretulias Ulias* Mioc. NA., *Metopocetus* Mioc. NA. Eu., *Aglaocetus Palaeobalaena* Mioc. SA., *Cetotheriopis* [*Aulocelus*] Mioc. SA. Eu., *Aulocetus Cetotheriomorphus Eucetotherium Herpetocetus Pachyacanthus* Mioc. Eu., *Cetotherium Isocetus Mesocetus* Mioc. Eu. ?NA., *Plesiocetopsis* [*Plesiocetus*] Mioc. NA. SA., Plioc. Eu., *Amphicetus Heterocetus* Plioc. Eu., *Nannocetus* Plioc. NA. **F. Rhachianectidae,** R. Oc., *Rhachianectes* Pleist. Eu., R. Oc. **F. Balaenopteridae,** R. Oc., *Mesoteras* Mioc. NA., *Burtinopsis Cetotheriophanes Idiocetus Megapteropsis Plesiocetus* Plioc. Eu., *Balaenoptera* Plioc.–Pleist. Eu. NA., R. Oc., *Megaptera* Plioc. Eu., Plioc.–Pleist. NA., R. Oc. **F. Balaenidae,** R. Oc., *Morenocetus* Mioc. SA., *Balaenotus Balaenula Palaeocetus Protobalaena* Plioc. Eu., *Balaena* Plioc.–Pleist. Eu., R. Oc., *Notiocetus* Plioc. SA., *Eubalaena* Pleist. SA., R. Oc.

Order Rodentia

SUBORDER SCIUROMORPHA

SUPERFAMILY APLODONTOIDEA. **F. Ischyromyidae,** *Paramys* Paleoc.–Eoc. NA., Eoc. Eu., *Ischyrotomus Leptotomus Mysops Pareumys Pseudotomus Rapamys Reithroparamys Sciuravus Taxymys Tillomys* Eoc. NA., *Plesiarctomys* Eoc. Eu., *?Plesiospermophilus ?Sciurodon* Eoc.–Olig. Eu., *Cylindrodon Ischyromys Manitscha Pseudocylindrodon ?Sespemys Titanotheriomys* Olig. NA., *Ardynomys Prosciurus* Olig. NA. As., *Cyclomys ?Tsaganomys* Olig. As., *?Kansasimys* Plioc. NA. **F. Aplodontidae,** R. NA. As., *Eohaplomys* Eoc. NA., *Allomys Haplomys Meniscomys* Mioc. NA., *Liodontia* Mioc.–Plioc. NA., *Aplodontia* [*Pseudaplodon*] Plioc.–R. As., Pleist.–R. NA. **F. Mylagaulidae,** *Eutypomys* Olig. NA., *Ceratogaulus Mesogaulus Mylogaulodon Promylagaulus* Mioc. NA., *Mylagaulus* Mioc.–Plioc. NA., *Epigaulus* Plioc. NA. **F. Protoptychidae,** *Protoptychus* Paleoc.–Eoc. NA. **F. Eomyidae,** *Protadjidaumo* Eoc. NA., *Eomys* Eoc.–Olig. Eu., *Adjidaumo Paradjidaumo* Olig. NA., *Omegodus Rhodanomys* Mioc. Eu.

SUPERFAMILY SCIUROIDEA. **F. Sciuridae,** R. Eu. As. Af. NA. SA., *Palaearctomys* Mioc. NA., *Citellus* [*Spermophilus*] Mioc.–R. NA., Pleist.–R. Eu. As., *Pteromys* ?Mioc.–R. Eu., Pleist.–R. As., *Sciurus* Mioc.–R. Eu. NA., Plioc.–R. As., Pleist.–R. SA., *Marmota* [*Arctomys*] Plioc.–R. NA., Pleist.–R. Eu. As., *Tamias* [*Eutamias*] Plioc.–R. NA. As., *Sciurotamias* Plioc.–R. As., *Otospermophilus* ?Plioc., Pleist.–R. NA., *Cynomys Glaucomys Tamasciurus* Pleist.–R. NA., *Petaurista* Pleist.–R. As. EInd., R. Eu., *Ratufa* Pleist.–R. EInd., R. SAs. **F. Castoridae,** R. Eu. As. NA., *Agnotocastor* Olig. NA., *Steneofiber* ?Olig., Mioc. Eu., *Euhapsis Hystricops Palaeocastor* Mioc. NA., *Amblycastor* Mioc. NA., Mioc.–Plioc. As., *Anchitheriomys Palaeomys* Mioc. Eu., *Chalicomys* Mioc.–Plioc. Eu., *Monosaulax* Mioc. ?Plioc. NA., ?Mioc. Eu., *Sinocastor* Plioc. As., *Dipoides* Plioc. Eu. As. NA., *Eucastor* Plioc. NA., *Trogontherium* Plioc.–Pleist. Eu., ?Pleist. As., *Castor* Plioc.–R. Eu. As. NA., *Castoroides Eucastoroides Procastoroides* Pleist. NA.

SUPERFAMILY GEOMYOIDEA. **F. Geomyidae,** R. NA. CA., *Diplolophus* Olig. NA., *Dikkomys Entoptychus Grangerimus Gregorymys Pleurolicus* Mioc. NA., *Thomomys* ?Mioc. ?Plioc., Pleist.–R. NA., *Geomys* Mioc.–R. NA., *Pliosaccomys* Plioc. NA., *Nerterogeomys* Plioc.–Pleist. NA., *Plesiothomomys* Pleist. NA., *Cratogeomys* Pleist.–R. NA. **F. Heteromyidae,** R. NA. SA., *Heliscomys* Olig.–Mioc. NA., *Florentiamys Mookomys Peridomys Proheteromys* Mioc. NA., *Diprionomys Perognathoides* Mioc.–Plioc. NA., *Perognathus* Mioc.–R. NA., *Cupidinimus Prodipodomys* Plioc. NA., *Dipodomys Liomys* Plioc.–R. NA., *Etadonomys* Pleist. NA., *Dipodomys* Pleist.–R. NA.

SUPERFAMILY BATHYERGOIDEA. **F. Bathyergidae,** R. Af., *?Cyclomylus ?Tsaganomys* Olig. As., *?Bathyergoides* Mioc. Af., *Gypsorhynchus* Pleist. Af., *Cryptomys Georychus* Pleist.–R. Af.

SUBORDER HYSTRICOMORPHA

SUPERFAMILY ANOMALUROIDEA. **F. Pseudosciuridae,** *Pseudosciurus* Eoc. Eu., *Sciuroides Suevosciurus* Eoc.–Olig. Eu. **F. Theridomyidae** *Theridomys Trechomys* Eoc.–Olig. Eu., *Altinomys Archaeomys Issiodoromys Nesokerodon Pararchaeomys Protechimys* Olig. Eu., *?Metaphiomys Phiomys* Olig. Af., *?Karakoromys* Olig. As., *?Apodecter ?Diamantomys ?Paraphiomys ?Phthinylla ?Pomonomys* Mioc. Af., *?Anomalomys* Mioc. Eu. **F. Pedetidae,** R. Af., *Parapedetes* Mioc. Af., *Pedetes* Pleist.–R. Af. **F. Anomaluridae,** R. Af.

SUPERFAMILY HYSTRICOIDEA. **F. Hystricidae,** R. Eu. As. Af., *Sivacanthion* Plioc. As., *Hystrix* Plioc.–R. Eu. As., Pleist.–R. Af., *Atherurus* Pleist.–R. Af. **F. Thryonom-**

yidae, R. Af., *Neosciuromys ?Phiomyoides* Mioc. Af., *?Peraulacodus* Plioc. As., *Thryonomys* Pleist.–R. Af. **F. Petromyidae,** R. Af., *Petromys* Pleist.–R. Af. **?F. Ctenodactylidae,** R. Af., *Tataromys* Olig. EAs., *Sayimys Pectinator* Plioc. As., R. Af. **F. Erethizontidae.,** R. NA. SA., *Asteromys Eosteiromys Parasteiromys Protacaremys* Olig. SA., *Acaremys Steiromys* Olig.–Mioc. SA., *Sciamys* Mioc. SA., *Erethizon* ?Plioc., Pleist.–R. NA., *Coendu* Pleist.–R. SA., R. CA., *Chaetomys* Pleist.–R. SA. **F. Caviidae,** R. SA. CA. WInd., *Archaeocardia* [*Palaeocardia*] *Cephalomys Litodontomys Lutantus* Olig. SA., *Callodontomys Dicardia Eocardia Hedimys ?Neoreomys Phanomys Procardia Schistomys Tricardia* Mioc. SA., *Cardiomys* ?Mioc., Plioc. SA., *Anchimys Anchimysops Cardiatherium Dolicavia Eucardiodon* ["*Cardiodon*"] *Hydrochoeropsis Macrocavia Neocavia Neoprocavia Nothydrochoerus Orthomyctera Palaeocavia Parodimys Phagatherium Plexochoerus Pliodolichotis Procardiotherium Prodolicotus Prohydrochoerus Protohydrochoerus* Plioc. SA., *Neochoerus* Pleist. NA., *Hydrochoerus* Pleist. NA., Pleist.–R. SA., *Cavia Coelogenys* [*Cuniculus*] *Dolichotis Galea Microcavia* Pleist.–R. SA., *Dasyprocta* Pleist.–R. SA., R. WInd. **F. Octodontidae,** R. SA. WInd., *Eoctodon Protadelphomys* Olig. SA., *Spaniomys* Olig.–Mioc. SA., *Adelphomys Graphimys Lomomys Paramyocastor Scleromys* Mioc. SA., *Proechimys* Mioc.–R. SA., *Colpostemma Dicoelophorus Discolomys Eucoelophorus Eumysops Gyrignophus Haplostropha Isomyopotamus Megactenomys Morenia Neophanomys Palaeoctodon Phthoramys Pithanotomys Plataeomys Prospaniomys Protabrocoma Pseudoplataeomys Stichomys Strophostephanus Tramyocastor Xenodontomys* Plioc. SA., *Abrocoma Myocastor* Plioc.–R. SA., *Carterodon Dicolpomys Drytomomys Mesomys Ronchophorus* Pleist. SA., *Alterodon Aphaetreus Boromys Brotomys Heteropsomys Hexolobodon Homopsomys Isolobodon Ithydontia* Pleist. WInd., *Capromys Geocapromys Plagiodontia* Pleist.–R. WInd., *Cercomys Echimys Kannobateomys* Pleist.–R. SA. **F. Dinomyidae,** R. SA., *Simplimus* Mioc. SA., *?Olenopsis Phoberomys* Mioc.–Plioc. SA., *Carlesia Dabbenea Diaphoromys Gyriabrus Isostylomys Neoepiblema Pentastylomys Potamarchus Protomegamys Pseudosigmomys Rusconia Telicomys Telodontomys Tetrastylomys Tetrastylopsis Tetrastylus* Plioc. SA., *Eumegamys* ["*Megamys*"] Plioc.–Pleist. SA., *Amblyrhiza Clidomys Elasmodontomys Heptaxodon Quemisia Speoxenus Spirodontomys* Pleist. WInd. **F. Chinchillidae,** R. SA., *Perimys Pliolagostomus Prolagostomus Scotaeumys Sphaeromys* Olig.-Mioc. SA., *?Eusigmomys* Mioc. SA., *Briaromys Euphilus Lagostomopsis* Plioc. SA., *Lagidium Lagostomus* Pleist.–R. SA.

SUBORDER MYOMORPHA

SUPERFAMILY DIPODOIDEA. **F. Zapodidae,** R. Eu. As. NA., *Plesiosminthus* Olig. Eu., *Pliozapus* Plioc. NA., *Heterosminthus* Plioc. As., *Napaeozapus Zapus* Pleist.–R. NA., *Sicista* Pleist.–R. Eu., R. As. **F. Dipodidae,** R. Eu. As. Af., *?Sciuromys* Eoc. Olig. Eu., *Protalactaga* Mioc.–Plioc. As., *Brachysaitetes Paralactaga Plesiodipus Sminthoides* Plioc. As., *Allactaga* Plioc.–R. As., Pleist.–R. Eu., R. NAf., *Dipus* Pleist.–R. As., R. Eu.

SUPERFAMILY MUROIDEA. **F. Myoxidae (Gliridae, Muscardinidae),** R. Eu. As. Af., *Gliravus* Olig. Eu., *Heteromyoxus* Mioc. Eu., *Dryomys* Mioc.–R. Eu., *Eliomys* Mioc.–R. Eu., R. NAf. WAs., *Myoxus* [*Glis*] Mioc.–R. Eu., R. WAs., *Amphidryomys* Plioc. Eu., *Leithia* Pleist. Malta, *Hypnomys* Pleist. Balaeric Is., *Philistomys* Pleist. WAs., *Muscardinus* Pleist.–R. Eu., R. WAs. **F. Muridae,** R. Cos., *?Simimys* Eoc. NA., *Scottimus* Olig. NA., *Eumys* Olig. NA. As., *Aralomys Eumysodon* Olig. WAs., *Cricetops Selenomys* Olig. As., *Cricetodon* Olig. As. NA., Olig.–Mioc. Eu., *Schaubeumys* Olig. As., Mioc. NA., *Heterocricetodon Paracricetodon*

Olig. Eu., *Leidymys* Olig.–Mioc. NA., *Horatiomys Palustrimus Poamys* Mioc. NA., *?Anomalomys ?Melissiodon* Mioc. Eu., *Prosiphneus* Mioc.–Plioc. As., *Bensonomys Copemys Cosomys Goniodontomys Macrognathomys Neondatra* Plioc. NA., *Allophaiomys Anthracomys Baranomys Germanomys Trilophomys Ungaromys* Plioc. Eu., *Acomys* Plioc. Eu., R. Af. WAs., *Lagurus* Plioc. Eu., R. As. NA., *Neocricetodon Progonomys Stephanomys* Plioc. Eu. As., *Anatolomys Kanisamys Lophocricetus Microtodon Microtoscoptes Myotalpavus Nannocricetus Paracricetulus Plesiocricetodon Pseudomeriones Sinocricetus* Plioc. As., *Parapodemus* Plioc. As., Plioc. Pleist. Eu., *Cricetus* ?Plioc., Pleist.–R. As., Plioc.–R. Eu., *Cricetulus* Plioc.–R. As., Pleist.–R. Eu., *Cleithrionomys* Plioc.–R. Eu., Pleist.–R. As. NA., *Gerbillus* Plioc.–R. As., R. Af., *Hesperomys* Plioc.–R. SA., *Mastomys* Plioc.–R. As., *Mimomys* Plioc.–Pleist. Eu., Pleist. As. NA., *Myospalax* [*Myotalpa Siphneus*] Plioc.–R. As., *Peromyscus* Plioc.–R. NA., *Sigmodon* ?Plioc. As., Pleist.–R. SA. NA., *Apodemys* Plioc.–R. Eu., Pleist.–R. As., R. Af., *Anaptogonia Baiomys Ogmodontomys Parahodomys Pliolemnus Pliopotamys Sycium Symmetrodontomys* Pleist. NA., *Eligmodontia* Pleist. NA., R. SA., *Bothriomys Necromys Ptyssophorus* Pleist. SA., *Mirus Rhagamys Tyrrhenicola* Pleist. Eu., *Allocricetus* Pleist. Eu. WAs., *Phodopus* Pleist. Eu. R. As., *Cricetinus* Pleist. As., *Coryphomys* Pleist. EInd., *Majoria* Pleist. Mad., *Megalomys* Pleist. WInd., *Mus* Pleist. Crete, Cyprus, Pleist.–R. Eu. As., R. Cos., *Rattus* [*Epimys*] Pleist. Crete, Pleist.–R. As., R. Cos., *Neofiber Neotoma Ondatra Onychomys Phenacomys Reithrodontomys Synaptomys* Pleist.–R. NA., *Oryzomys* Pleist.–R. NA. SA., *Akodon Blarinomys Holochilus Oxymycterus Reithrodon Rhipidomys Scapteromys Zygodontomys* Pleist.–R. SA., *Dolomys* Pleist.–R. Eu., *Pitymys* Pleist.–R. Eu. As. NA., *Arvicola Evotomys* Pleist.–R. Eu. As., *Dicrostonyx Lemmus* [*Myodes*] Pleist.–R. Eu. As., R. NA., *Microtus* Pleist.–R. Eu. As. NA., R. NAf., *Alticola Eothenomys Tatera* Pleist.–R. As., *Leggada* Pleist.–R. As. Af., *Mesocricetus* Pleist.–R. As., R. Eu., *Arvicanthis* Pleist.–R. WAs. Af., *Golunda Nesokia* Pleist.–R. SAs., R. NAf., *Jaculus Lophuromys Otomys Saccostomus* Pleist.–R. Af., *Ellobius* [*Bramus*] Pleist.–R. NAf., R. Eu. WAs., *Meriones* Pleist.–R. NAf., R. WAs., *Hydromys* Pleist.–R. Aus., *Lenomys* Pleist.–R. EInd., *Hypogeomys Macrotarsomys* Pleist.–R. Mad. **F. Spalacidae,** R. Eu. As. NAf., *Rhizospalax* Olig. Eu., *Tachyoryctoides* Olig. As., *Pararhizomys Protachyoryctes* Plioc. As., *Pliospalax* Plioc. Eu., *Prospalax* Plioc.–Pleist. Eu., *Rhizomys* Plioc.–R. As., *Tachyoryctes* Pleist.–R. Af., *Spalax* Plioc.–R. Eu., Pleist.–R. As., R. NAf.

ORDER LAGOMORPHA. **F. Eurymylidae,** *Eurymylus* Paleoc. As. **F. Ochotonidae,** R. Eu. As. NA., *Titanomys* Olig.–Mioc. Eu., *Austrolagomys* Mioc. Af., *Lagopsis* Mioc. Eu., *Prolagus* Mioc.–Pleist. Eu., *Ochotonoides* Plioc.–Pleist. As., *Ochotona* [*Proöchotona*] Plioc.–R. Eu. As., Pleist.–R. NA. **F. Leporidae,** R. Eu. As. Af. NA. SA., *Mytonolagus* Eoc. NA., *Shamolagus* Eoc. As., *Gobiolagus* Eoc.–Olig. As., *Archaeolagus Palaeolagus* Olig. NA., *Desmatolagus* Olig. NA. As., *Sinolagomys* Olig. As., *Amphilagus Piezodus* Olig. Eu., *Oreolagus* Mioc. NA., *Hypolagus* Mioc.–Pleist. NA., Plioc.–Pleist. Eu. As., *Dicea Notolagus Pediolagus Pratilepus* Plioc. NA., *Pliolagus* Plioc. Eu. As., *Allolagus* Plioc. As., *Alilepus* Plioc.–Pleist. As., Pleist. NA., *Caprolagus* Plioc. Eu., Plioc.–R. As., *Nekrolagus* Plioc.–Pleist. NA., *Lepus* Plioc.–R. Eu. As. Af., Pleist.–R. NA., *Oryctolagus* Plioc.–R. Eu., Pleist.–R. Af., *Pronolagus* Pleist.–R. Af., *Sylvilagus* Pleist.–R. SA. NA.

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The books and papers listed below include but a small proportion of even the more fundamental and important works dealing with fossil vertebrates. Special emphasis has been given to comprehensive monographs, bibliographic sources, and well-illustrated descriptions of typical forms. Some notes regarding workers in the field have been included.

Vertebrate paleontology was essentially founded by Cuvier somewhat over a century ago. As a comparative anatomist he studied petrefactions in the light of his knowledge of modern types. Much of his work is summarized in his *Ossemens fossiles* (No. 4). Sir Richard Owen, working somewhat later in the nineteenth century, was, again, a comparative anatomist and the first English paleontologist of importance. Von Meyer, his contemporary, published many fine works on German fossils, and Agassiz's important work on fossil fishes (No. 29) also dates from the first half of the century. Neither Cuvier, Owen, nor Agassiz believed in evolution. Darwin did no original work in paleontology, but the acceptance of his theories gave a new point to the study of fossils and led to a wide expansion of the field.

In America little work was done until exploration had opened up the great western fossil country. Joseph Leidy, the anatomist, whose active career in the field of paleontology was mainly between 1850 and 1875, was the first American worker of importance. In the late sixties Cope of Philadelphia and Marsh of New Haven entered the field and dominated it until the closing years of the century; Osborn, Scott, and Williston began work in the eighties.

GENERAL WORKS

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   This useful work covers both invertebrates and vertebrates. The last German edition of Volume 2 (*Vertebrata*), revised by Broili and Schlosser, was published in 1923. An English translation, revised by Sir Arthur Smith Woodward, is published in two volumes, that on lower vertebrates in 1932, that on mammals in 1925.
2. Abel, O. 1919. *Die Stämme der Wirbeltiere.* Berlin and Leipzig. Pp. 914.
   Contains numerous useful illustrations, particularly of fishes and reptiles.
3. Lull, R. S. 1929. *Organic Evolution.* 2d ed. New York. Pp. 762.
   Good elementary accounts of a number of vertebrate groups, including dinosaurs and several mammalian orders. A new edition is in preparation (1945).
4. Cuvier, G. 1834–36. *Recherches sur les ossemens fossiles, où l'on rétablit les caractères de plusieurs animaux dont les révolutions du globe ont détruit les espèces.* 4th ed. 10 vols.+2 vols. pls. Paris.
   The first great paleontological work. First issued in 1812.
5. Abel, O. 1912. *Grundzüge der Palaeobiologie der Wirbeltiere.* Stuttgart. Pp. 703.
   A stimulating study of adaptations in living and fossil vertebrates.
6. ———. 1927. *Lebensbilder aus der Tierwelt der Vorzeit.* 2d ed. Jena. Pp. 714.
   Interesting discussion of a number of representative faunas from Permian to Pleistocene.
7. ———. 1929. *Paläobiologie und Stammesgeschichte.* Jena. Pp. 423.
8. Stromer, E. 1912. *Lehrbuch der Paläozoologie,* Vol. 2: *Wirbeltiere.* Leipzig and Berlin. Pp. 325.
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11. Boule, M., and Piveteau, J. 1935. *Les fossiles: éléments de paléontologie.* Paris. Pp. 899.
A systematic account of the faunas of successive eras.

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A few general sources are noted here; other more restricted bibliographies are cited under the various groups.

12. *Neues Jahrbuch für Mineralogie, Geologie und Palaeontologie.* 1830——. Stuttgart.
Contains critical reviews of practically all the paleontological literature of the past century. Index volumes have been published at irregular intervals.

13. *Palaeontologisches Zentralblatt.* 1932——.
Abstracts of the literature since 1932.

14. *Zoölogical Record.* 1864——. London.
A year-by-year bibliography of all zoölogical papers, arranged taxonomically. The literature on fossils is well covered in the more recent volumes, less so in the earlier issues.

15. *Biological Abstracts.* 1926——. Philadelphia.
Covers all biological literature, including paleontology.

16. Hay, O. P. 1902. "Bibliography and Catalogue of the Fossil Vertebrata of North America," *Bull. U.S. Geol. Surv.*, No. 179. Pp. 868.

16*a*. ———. 1929. *Second Bibliography*. . . . . 2 vols. *Pub. Carnegie Inst. Washington*, No. 390. Pp. 2003.
These works list every citation, to the year 1927, of every American fossil form, together with the general literature on every group ever present in North America. Comparable bibliographies of non-American forms are in preparation.

17. Camp, C. L., and Others. 1940. "Bibliography of Fossil Vertebrates, 1928–33," *Geol. Soc. Amer., Spec. Papers*, No. 27. Pp. 503. A second volume covering the years 1934–38 was issued in 1942. *Geol. Soc. Amer., Spec. Papers*, No. 42. Pp. 663.
Covers the world literature, in continuation of Hay.

18. Quenstedt, W. (ed.). 1913——. "Fossilium catalogus, I, Animalia." Berlin and The Hague.
This series is planned to include eventually bibliographies of all fossil forms; about twenty parts dealing with vertebrates have been published.

VERTEBRATE STRUCTURE

19. Bolk, L., and Others. 1931–38. *Handbuch der vergleichenden Anatomie der Wirbeltiere.* 6 vols. Berlin and Vienna.
A comprehensive work on vertebrate anatomy by a large number of specialists.

20. Parker, T. J., and Haswell, W. A. 1940. *A Text-Book of Zoölogy*, Vol. 2. Revised by C. Forster-Cooper. 6th ed. London. Pp. 758.

21. Versluys, J., and Others. 1927. *Vergleichende Anatomie der Wirbeltiere.* Berlin. Pp. 906.
A sound, comprehensive, and up-to-date work. The chapter on the skeleton (by Versluys) takes the fossil forms into account.

22. Neal, H. V., and Rand, H. W. 1936. *Comparative Anatomy.* Philadelphia. Pp. 739.

23. Hyman, L. H. 1942. *Comparative Vertebrate Anatomy.* 2d ed. Chicago. Pp. 544.

24. Goodrich, E. S. 1930. *Studies on the Structure and Development of Vertebrates.* London. Pp. 907.
Excellent discussion of many problems dealing with the skull, backbone, fins, etc., in lower vertebrates.

25. Reynolds, S. H. 1913. *The Vertebrate Skeleton.* 2d ed. Cambridge. Pp. 535.

A standard work, prepared from the paleontologist's point of view, although dealing primarily with living forms.

26. Edinger, T. 1929. "Die fossilen Gehirne," *Ergeb.-Anat. u. Entwickl.*, Vol. **28.** Pp. 249.

Endocranial structure in all vertebrate classes. A supplement in *Fortschr. d. Pal.*, 1: 235–51 (1937).

27. Gregory, W. K. 1929. *Our Face from Fish to Man.* New York. Pp. 295.

Evolution of cranial structure in fossil and recent forms from fish through primitive tetrapods to mammals. A more comprehensive work on vertebrate evolution by this author is in preparation (1945).

LOWER CHORDATES

28. Delage, V., and Hérouard, E. 1898. *Traité de zoologie concrète*, Vol. 8: *Les Procordés.* Paris. Pp. 379+54 pls.

Detailed and well-illustrated description of structure and development of lower chordates.

No. 22 gives a concise account.

FISHES, GENERAL

The first comprehensive study of fossil fishes was that of Louis Agassiz, nearly a century ago (No. 29). A more recent thorough survey of the field is that of Smith Woodward (No. 30). With these two workers should be ranked Traquair, who published many important papers on Scotch Paleozoic fishes during the latter decades of the nineteenth century; and no mention of fossil fishes could be made without reference to Hugh Miller, the Scottish stonemason, who collected much of the Old Red Sandstone material studied by Agassiz and published several volumes compounded of paleontology, theology, and homely philosophy. Among the comparatively few American workers who devoted themselves mainly to fishes may be mentioned Newberry, Dean, Eastman, and Patten. Among later European workers may be mentioned Pander and Rohon, older Russian workers on Paleozoic material; Leriche, Priem, and Sauvage in France; Hennig and the erratic but brilliant Jaekel in Germany; Watson in England; and Stensiö of Stockholm, the last two of whom have contributed greatly to our present concepts of fish history. Among current or younger recent workers (particularly active on Paleozoic groups) we may note: Aldinger, Arambourg, Broili, Brotzen, Brough, Bryant, David, Dunkle, Graham-Smith, Gross, Heintz, Hills, Jarvik, Moy-Thomas, Nielsen, Obrutschev, Piveteau, Rayner, Robertson, Säve-Söderbergh, Weigelt, Weiler, Weitzel, Westoll, and E. I. White.

29. Agassiz, L. 1833–44. *Récherches sur les poissons fossiles.* 5 vols. Pp. 1420+369 pls. With supplement, *Monographie des poissons fossiles du vieux grès rouge ou système Dévonien (Old Red Sandstone)des Iles Britanniques et de Russie.* Neuchatel. Pp. 171+43 pls.

An account of all forms known at that time. While the text is antiquated, the numerous colored plates are still very valuable.

30. Woodward, A. Smith. 1889–1901. *Catalogue of the Fossil Fishes in the British Museum.* 4 vols. London. Pp. 2493+70 pls.

Not merely a catalogue; in reality a summary of our knowledge of fossil fishes to the date of publication. It is still extremely useful, especially for Mesozoic and Tertiary forms.

31. Dean, B. 1916–23. *A Bibliography of Fishes.* 3 vols. New York. Pp. 2160.

A complete bibliography of all works on fishes, recent and fossil. An author list, with comprehensive indexes.

32. GOODRICH, E. S. 1909. *A Treatise on Zoölogy* (ed. E. RAY LANKESTER), Part IX: *Vertebata craniata*, Fasc. I: "Cyclostomes and Fishes." London. Pp. 534.

An excellent account of fishes, living and fossil, with particular attention to morphology. Still good except for some Paleozoic groups.

33. BERG, L. S. 1940. "Classification of Fishes, both Recent and Fossil," *Trav. Inst. Zool. Acad. Sci. U.R.S.S.*, Vol. 5, Part II. Pp. 517.

34. GREGORY, W. K. 1933. "Fish Skulls: A Study of the Evolution of Natural Mechanisms," *Trans. Amer. Phil. Soc.*, **23**: 75–481.

Particularly teleosts.

35. MOY-THOMAS, J. A. 1939. *Palaeozoic Fishes.* London and New York. Pp. 149.

An excellent and up-to-date account.

36. ROMER, A. S., and GROVE, B. H. 1935. "Environment of the Early Vertebrates," *Amer. Mid. Nat.*, **16**:805–56.

Fresh- versus salt-water origin.

AGNATHA

Our older knowledge of ostracoderms was due in great measure to Lankester and particularly to Traquair. Among recent workers may be mentioned Stensiö, Kiaer, Bryant, Heintz, Robertson, Stetson, and E. I. White.

37. STENSIÖ, E. A. 1927. "The Downtonian and Devonian Vertebrates of Spitzbergen. I. Family Cephalaspidae," *Skr. om Svalbard og Nordishavet*, No. 12. 2 vols. Pp. 391+112 pls.

An exhaustive study of the cranial structure of the Osteostraci, with an account of previous work and a discussion of the structure and relationships of all the agnathous types. The next is a companion volume.

38. ———. 1932. *The Cephalaspids of Great Britain.* London. Pp. 220+66 pls.

39. HEINTZ, A. V. 1939. "Cephalaspida from Downtonian of Norway," *Skr. norsk. vidensk.-Akad. i Oslo, mat.-nat. Kl.*, No. 5. Pp. 119.

40. ROBERTSON, G. M. 1938. "The Tremataspidae," *Amer. Jour. Sci.*, 5th ser., **35**:172–206, 273–96.

41. KIAER, J. 1924. "The Downtonian Fauna of Norway. I. *Anaspida.*" *Skr. vidensk. selsk. Kristiania, mat.-nat. Kl.*, Vol. 1, No. 6. Pp. 139.

First discovered by Traquair in the late nineties, the anaspids became adequately known only as a result of Kiaer's work. A thorough description of the morphology and evolutionary significance of typical anaspids.

42. STENSIÖ, E. A. 1939. "A New Anaspid from the Upper Devonian of Scaumenac Bay in Canada, with Remarks on the Other Anaspids," *Handl. k. svensk. vetensk. Akad.*, 3d ser., Vol. 18. Pp. 25.

43. KIAER, J. 1932. "The Downtonian and Devonian Vertebrates of Spitsbergen. IV. Suborder Cyathaspida," *Skr. om Svalbard og Ishavet*, No. 52. Pp. 26.

Detailed account of primitive Heterostracans.

44. BRYANT, W. L. 1936. "A Study of the Oldest Known Vertebrates: *Astraspis* and *Eriptychius*," *Proc. Amer. Phil. Soc.*, **76**, No. 4, 409–27.

On the fragmentary Ordovician material.

45. WHITE, E. I. 1935. "The Ostracoderm *Pteraspis* Kner and the Relationships of the Agnathous Vertebrates," *Phil. Trans. Roy. Soc. London*, B, **225**:381–457.

46. KIAER, J. 1932. "New Coelolepids from the Upper Silurian on Oesel (Esthonia)," *Arch. naturk. Estlands*, 1st ser., **10**:169–74.

ACANTHODIANS

47. Watson, D. M. S. 1937. "The Acanthodian Fishes," *Phil. Trans. Roy. Soc. London*, B, **228**:49–146.

Includes a stimulating discussion of the position of the other groups of placoderms (Aphetohyoidea).

ARTHRODIRES

The earlier work on this group was mainly done by Pander and Traquair in Europe, and by Newberry, Dean, and Hussakof in America. Heintz, Gross, Watson, Stensiö, and Dunkle are recent writers in this field.

48. Heintz, A. 1929. "Die downtonischen und devonischen Vertebraten von Spitsbergen. II. Acanthaspida," *Skr. om Svalbard og Ishavet*, No. 22. Pp. 81. *Nachtrag*. Pp. 20.

Primitive early Devonian forms.

49. ———. 1931. "Untersuchungen über den Bau der Arthrodira," *Acta zool.*, **12**:225–39.

General account of the group.

50. ———. 1931. "Revision of the Structure of *Coccosteus decipiens* Ag.," *Norsk geol. tidsskr.*, **12**:291–313.

51. Stensiö, E. A. 1934. "On the Heads of Certain Arthrodires. I. *Pholidosteus*, *Leiosteus*, and Acanthaspids," *Handl. k. svensk. vetensk. Akad.*, Vol. **13**, No. 5. Pp. 79.

52. Watson, D. M. S. 1934. "The Interpretation of Arthrodires," *Proc. Zoöl. Soc. London*, 1934, pp. 437–64.

53. Heintz, A. 1938. "Notes on Arthrodira," *Norsk geol. tidsskr.* Vol. **18**. Pp. 27.

54. ———. 1932. "The Structure of *Dinichthys:* A Contribution to Our Knowledge of the Arthrodira," *Bashford Dean Memorial Volume*. New York. Pp. 115–224+9 pls.

A comprehensive account of Cleveland shale arthrodires by Dunkle is in preparation (1945).

55. ———. 1934. "Revision of the Estonian Arthrodira. I. Family Homostiidae Jaekel," *Pub. Geol. Inst. Univ. Tartu*, No. 38. Pp. 114.

56. Watson, D. M. S. 1938. "On *Rhamphodopsis*, a Ptyctodont from the Middle Old Red Sandstone of Scotland," *Trans. Roy. Soc. Edinburgh*, **59**:397–410.

ANTIARCHS

57. Stensiö, E. A. 1931. "Upper Devonian Vertebrates from East Greenland," *Meddel. om Grønland*, Vol. **86**, No. 1. Pp. 207.

A thorough description of *Bothriolepis* and *Remigolepis* and a general consideration of the position of the group. A new work by Stensiö is in press (1945).

58. Gross, W. 1931. "*Asterolepis ornata* Eichw. und das Antiarchi-Problem," *Palaeontogr.*, **75**:1–62.

59. ———. 1941. "Die *Bothriolepis*-Arten der Cellulosa-Mergel Lettlands," *Handl. k. svensk. vetensk. Akad.*, 3d ser., Vol. **19**, No. 5. Pp. 79.

60. Denison, R. H. 1941. "The Soft Anatomy of *Bothriolepis*," *Jour. Pal.*, **15**, No. 5, 553–61.

MACROPETALICHTHYIDA

61. Stensiö, E. A. 1925. "On the Head of the Macropetalichthyids, with Certain Remarks on the Head of the Other Arthrodires," *Field Mus. Nat. Hist., Geol. Ser.*, **4**, No. 4, 87–197.

62. Broili, F. 1930. "Neue Beobachtungen an *Lunaspis*," *Sitz.-Ber. Akad. Wiss. München*, 1930, Part I, pp. 47–57.

63. Gross, W. 1933–37. "Die Wirbeltiere des rheinischen Devons," *Abh. preuss. geol. Landesanst.*, new ser., No. 154, pp. 1–83; No. 176, pp. 1–83.

Identifies *Lunaspis* as a placoderm related to *Macropetalichthys*. Fauna includes other placoderms and ostracoderms.

64. Heintz, A. 1937. "Die downtonischen und devonischen Vertebraten von Spitzbergen. VI. *Lunaspis*-Arten aus dem Devon Spitzbergens," *Skr. om Svalbard og Ishavet*, No. 72. Pp. 23.

STEGOSELACHIANS

65. Broili, F. 1930. "Ueber *Gemündina stürtzi*," *Abh. bavar. Akad. Wiss., math.-nat. Abt.*, new ser., **6**:1–24.

First described by Traquair; redescribed and restored in this paper and that following.

66. ———. 1933. "Weitere Fischreste aus den Hunsrückschiefern," *Sitz.-Ber. Akad. Wiss. München*, 1933, Part II, pp. 269–313.

67. ———. 1933. "Ein Macropetalichthyide aus den Hunsrückschiefern," *ibid.*, Part III, pp. 417–37.

The fish later named *Pseudopetalichthys*.

PALAEOSPONDYLUS

68. Moy-Thomas, J. A. 1940. "The Devonian Fish *Palaeospondylus gunni* Traquair," *Phil. Trans. Roy. Soc. London*, B, **230**:391–413.

The nature of this little fish has been much debated.

SHARKS

69. Moy-Thomas, J. A. 1939. "The Early Evolution and Relationships of the Elasmobranchs." *Biol. Rev.*, **14**:1–26.

An excellent review.

70. Dean, B. 1909. "Studies on Fossil Fishes (Sharks, Chimaeroids, and Arthrodires," *Mem. Amer. Mus. Nat. Hist.*, **9**:211–87.

Good illustrations of *Cladoselache* and late Devonian arthrodires.

71. Gross, W. 1937–38. "Das Kopfskelett von *Cladodus wildungensis* Jaekel," *Senckenbergiana*, **19**:80–107; **20**:123–45.

72. Moy-Thomas, J. A. 1936. "The Structure and Affinities of the Fossil Elasmobranch Fishes from the Lower Carboniferous Rocks of Glencartholm, Eskdale," *Proc. Zoöl. Soc. London*, 1936, pp. 761–88.

Ctenacanthus, Goodrichia, Tristychius, Oracanthus.

73. ———. 1935. "On the Carboniferous Shark, *Petrodus patelliformis* M'Coy," *Proc. Leeds Phil. Lit. Soc., Sci. Sect.*, **3**:68–72.

A Carboniferous hybodont. On *Hybodus*, see Woodward, No. 101.

74. Bigelow, H. B., and Schroeder, W. C. 1945. "Fishes of the Western North Atlantic," Vol. 1, No. 2: "Cyclostomes and Sharks."

In preparation (1945). An illustrated account of modern shark genera, many known as fossils.

75. Fowler, A. W. 1911. "A Description of the Fossil Fish Remains of the Cretaceous Eocene and Miocene Formations of New Jersey," *Bull. Geol. Surv. New Jersey*, **4**:22–182.

One of numerous illustrated accounts of shark teeth. For Cretaceous forms see Woodward, No. 103.

76. Jaekel, O. 1894. *Die eocänen Selachier vom Monte Bolca. Ein Beitrag zur Morphogenie der Wirbelthiere.* Berlin. Pp. 176+8 pls.

A number of Eocene forms are figured.

HOLOCEPHALI (INCLUDING BRADYODONTS)

77. Woodward, A. Smith. 1921. "Observations on Some Extinct Elasmobranch Fishes," *Proc. Linn. Soc. London, Sess.* 133, pp. 29–39.

The grouping of Paleozoic pavement-toothed fishes as bradyodonts was suggested in this paper. On bradyodonts see also No. 69.

78. De Beer, G. R., and Moy-Thomas, J. A. 1935. "On the Skull of Holocephali," *Phil. Trans. Roy. Soc. London*, B, **224**:287–312.
Fossil and recent chimaeras. For fossil teeth see also Woodward, No. 103, and Fowler, No. 75; see also Dean, No. 70.

79. Moy-Thomas, J. A. 1936. "On the Structure and Affinities of the Carboniferous Cochliodont *Helodus simplex*," *Geol. Mag.*, **73**:488–503.

80. Jaekel, O. 1899. "Ueber die Organization der Petalodonten," *Zeitschr. d. deutsch. geol. Gesellsch.*, **51**, 258–97. Particularly *Janassa*.

81. Davis, J. W. 1883. "On the Fossil Fishes of the Carboniferous Limestone Series of Great Britain," *Trans. Roy. Dublin Soc.*, 2d ser., **1**:327–548.
Teeth of many bradyodonts are figured.

82. Nielsen, E. 1932. "Permo-Carboniferous Fishes from East Greenland," *Meddel. om Grønland*, Vol. **86**, No. 3. Pp. 63.
Discusses tooth structure in bradyodonts and early sharks.

83. Moy-Thomas, J. A. 1935. "The Structure and Affinities of *Chondrenchelys problematica* Traquair," *Proc. Zoöl. Soc. London*, 1935, pp. 391–403.

LOWER ACTINOPTERYGIANS

Much valuable work has been done on palaeoniscoids and subholosteans in recent years by European workers, including, among others, Aldinger, Brough, Moy-Thomas, Nielsen, Waite, Watson, Westoll, and White.

84. Goodrich, E. S. 1927. "*Polypterus* a Palaeoniscid?" *Palaeobiol.*, **1**:87–92.

85. Traquair, R. H. 1877–1914. "The Ganoid Fishes of the British Carboniferous Formations," *Mono. Palaeontogr. Soc. London*. Pp. 186.
One of the most valuable older works on palaeoniscoids. For figures of late Carboniferous types, see Fritsch, No. 143.

86. Hennig, E. 1925. "*Chondrosteus hindenburgi* Pomp., ein "Stör" des württemberg. Oelschiefers (Lias)," *Palaeontogr.*, **67**:115–33.

87. Watson, D. M. S. 1925. "The Structure of Certain Palaeoniscids and the Relationships of That Group with Other Bony Fish," *Proc Zoöl. Soc. London*, 1925, pp. 815–70.

88. ———. 1928. "On Some Points in the Structure of Palaeoniscid and Allied Fish," *ibid.*, 1928, pp. 49–70.

89. Stensiö, E. A. 1932. "Triassic Fishes from East Greenland, Collected by the Danish Expeditions in 1929–31," *Meddel. om Grønland*, Vol. **83**, No. 3. Pp. 305.
Particularly *Saurichthys*.

90. Brough, J. 1936. "On the Evolution of Bony Fishes during the Triassic Period," *Biol. Rev.*, **11**:385–405.

91. Aldinger, H. 1937. "Permische Ganoidfische aus Ostgrönland," *Meddel. om Grønland*, Vol. **102**, No. 3. Pp. 392.
Discusses scale structure.

92. Nielsen, E. 1936. "Some Few Preliminary Remarks on Triassic Fishes from East Greenland," *Meddel. om Grønland*, Vol. **112**, No. 3. Pp. 55.

93. Moy-Thomas, J. A. 1937. "The Palaeoniscids from the Cement Stones of Tarras Waterfoot, Eskdale, Dumfriesshire," *Ann. Mag. Nat. Hist.*, 10th ser., **20**:345–56.

94. Westoll, T. S. 1937. "On the Cheek Bones in Teleostome Fishes," *Jour. Anat.*, **71**: 362–82.

95. White, E. I. 1927. "The Fish Fauna of the Cement Stones of Foulden, Berwickshire," *Trans. Roy. Soc. Edinburgh*, **55**:255–86.

96. Moy-Thomas, J. A., and Dyne, M. B. 1938. "The Actinopterygian Fishes from the

Lower Carboniferous of Glencartholm, Eskdale, Dumfriesshire," *Trans. Roy. Soc. Edinburgh*, **59**:437–80.
Numerous palaeoniscoids; good figures.

97. Brough, J. 1939. *The Triassic Fishes of Besano, Lombardy.* London: British Museum (Nat. Hist.). Pp. 117+7 pls.
Particularly subholosteans.

98. White, E. I. 1939. "A New Type of Palaeoniscoid Fish, with Remarks on the Evolution of the Actinopterygian Pectoral Fins," *Proc. Zoöl. Soc. London*, B, **109**:41–61.
Discusses actinopterygian fins.

99. Westoll, T. S. 1944. "The Haplolepidae, a New Family of Late Carboniferous Bony Fishes," *Bull. Amer. Mus. Nat. Hist.*, **83**:1–121.
With discussion of general aspects of early actinopterygian evolution.

100. Rayner, D. H. 1941. "The Structure and Evolution of the Holostean Fishes," *Biol. Rev.*, **16**:218–37.

101. Woodward, A. Smith. 1916–19. "The Fossil Fishes of the English Wealden and Purbeck Formations," *Mono. Palaeontogr. Soc. London.* Pp. 148.
Mainly holosteans, also *Leptolepis* and *Hybodus*.

102. Stensiö, E. A. 1935. "*Sinamia zdanskyi*, a new Amiid from the Lower Cretaceous of Shantung, China," *Pal. Sinica*, Ser. C, Fasc. I. Pp. 48.

TELEOSTEI

The literature on this group is abundant but scattered; much of the earlier work was brought together, however, in Woodward, No. 30. We give here a few examples of more comprehensive faunal papers.

103. Woodward, A. Smith. 1902–12. "The Fishes of the English Chalk," *Mono. Palaeontogr. Soc. London.* Pp. 264.
Mainly early teleosts, with many good figures.

104. Eastman, C. R. 1911. "Catalog of Fossil Fishes in the Carnegie Museum. I. Fishes from the Upper Eocene of Monte Bolca," *Mem. Carnegie Museum*, **4**, No. 7, 349–91. Also a supplement in the same series, **6**, No. 5, 315–48 (1914).

105. Arambourg, C. 1925. "Revision des poissons de *Licata* (Sicilie)," *Ann. pal.*, Vol. **14**, Pp. 96.

106. ———. 1927. "Les Poissons fossiles d'Oran," *Matériaux carte géol. d'Algérie*, Ser. 1, No. 6. Pp. 218.

107. David, L. R. 1943. "Miocene Fishes of Southern California," *Geol. Soc. Amer., Spec, Papers*, No. 43. Pp. 193.

108. Rayner, D. H. 1937. "On *Leptolepis bronni* Agassiz," *Ann. Mag. Nat. Hist.*, 10th ser., **19**:46–74.

109. Dunkle, D. H. 1940. "The Cranial Osteology of *Notelops brama* (Agassiz), an Elopid Fish from the Cretaceous of Brazil," *Lloydia*, **3**:157–90.

CROSSOPTERYGII AND DIPNOI

The classic figures of these forms are the plates of Agassiz (No. 29, Suppl.) and Pander (No. 110). The relationship of crossopterygians to tetrapods was particularly emphasized by Gregory and by Watson (No. 131) and in recent decades has been generally recognized (cf. Westoll, No. 129).

110. Pander, C. H. 1860. *Ueber die Saurodipterinen, Dendrodonten, Glyptolepiden und Cheirolepiden des devonischen Systems.* St. Petersburg. Pp. 89.
Good figures of Devonian specimens

111. Watson, D. M. S. 1935. "Fossil Fishes of the Orcadian Old Red Sandstone," in G. V. Wilson (ed.), *The Geology of the Orkneys* ("Mem. Geol. Surv. Scotland," 1935), pp. 157–69.
112. Westoll, T. S. 1937. "The Old Red Sandstone Fishes of the North of Scotland, Particularly of Orkney and Shetland," *Proc. Geol. Assoc. London*, **48**:13–45.
113. ———. 1936. "On the Structures of the Dermal Ethmoid Shield of *Osteolepis*," *Geol. Mag.*, **73**:157–71.
114. Romer, A. S. 1937. "The Braincase of the Carboniferous Crossopterygian *Megalichthys nitidus*," *Bull. Mus. Comp. Zoöl.*, Vol. **82**, No. 1. Pp. 73.
    See also *Jour. Morph.*, **69**, No. 1, 141–60 (1941).
115. Jarvik, E. 1937. "On the Species of *Eusthenopteron* Found in Russia and the Baltic States," *Bull. Geol. Inst. Univ. Upsala*, **27**:63–127.
116. Gregory, W. K., and Raven, H. C. 1941. "Studies on the Origin and Early Evolution of Paired Fins and Limbs," *Ann. New York Acad. Sci.*, **42**:273–360.
117. Watson, D. M. S. 1921. "On the Coelacanth Fish," *Ann. Mag. Nat. Hist.*, 9th ser., **8**:320–27. See also Woodward, No. 103.
118. Stensiö, E. A. 1921. *Triassic Fishes from Spitzbergen*. Part I. Wien. Pp. 307+35 pls. Especially coelacanths.
119. ———. 1937. "On the Devonian Coelacanthids of Germany with Special Reference to the Dermal Skeleton," *Handl. k. svensk. vetensk. Akad.*, 3d ser. Vol. **16**, No. 4. Pp. 56.
120. Moy-Thomas, J. A. 1937. "The Carboniferous Coelacanth Fishes of Great Britain and Ireland," *Proc. Zoöl. Soc. London*, B, **107**:383–415.
121. Schaeffer, B. 1941. "A Revision of *Coelacanthus newarki* and Notes on the Evolution of the Girdles and Basal Plates of the Median Fins in the Coelacanthini," *Amer. Mus. Novit.*, No. 1110. Pp. 17.
122. Dollo, L. 1895. "Sur la phylogénie des Dipneustes," *Bull. Soc. belge géol., pal. et hydrol.*, **9**:79–128.
    A brilliant essay in which the evolutionary trend of the lungfish series was first clearly demonstrated.
123. Watson, D. M. S., and Gill, E. L. 1923. "The Structure of Certain Palaeozoic Dipnoi," *Jour. Linn. Soc. London, Zoöl.*, **35**:163–216.
124. Forster-Cooper, C. 1937. "The Middle Devonian Fish Fauna of Achanarras," *Trans. Roy. Soc. Edinburgh*, **59**:223–39.
    On *Dipterus*.
125. Graham-Smith, W., and Westoll, T. S. 1937. "On a New Long-headed Dipnoan Fish from the Upper Devonian of Scaumenac Bay, P.Q., Canada," *Trans. Roy. Soc. Edinburgh*, **59**:241–66.
    Fleurantia.
126. Romer, A. S., and Smith, H. J. 1934. "American Carboniferous Dipnoans," *Jour. Geol.*, **42**:700–719.
127. Stromer, E. 1938. "Der Wüstenfisch *Ceratodus* Ag. 1838 und seine meso- und känozoischen Verwandten," *Neues Jahrb. Min., Geol. Pal.*, Beil.-Bd., Abt. B, **80**:248–63.

AMPHIBIA

The earlier finds of amphibians were principally described by Huxley (British material), Frič and Credner (Continental Europe), and Cope (America). Later workers included Broili, Broom, Case, Watson, and Williston; in recent years Bystrow, Nilsson, Olson, Säve-Söderbergh, Sawin, Steen, and J. A. Wilson. Particularly important in defining structural trends in the Amphibia are Nos. 130 and 131.

128. Kuhn, O. 1939. *Die fossilen Amphibien.* Berlin. Pp. 98.
Cf. review in *Jour. Pal.*, **14:**389–91.

129. Westoll, T. S. 1943. "The Origin of the Tetrapods," *Biol. Rev.*, **18:**78–98.

130. Watson, D. M. S. 1919. "The Structure, Evolution and Origin of the Amphibia—the 'Orders' Rachitomi and Stereospondyli," *Phil. Trans. Roy. Soc., London*, B, **209:**1–73.

131. ———. 1926. "The Evolution and Origin of the Amphibia," *ibid.*, **214:**189–257.

132. ———. 1930. "The Carboniferous Amphibia of Scotland," *Pal. Hungar.*, **1:**221–52.
Skulls of some of the oldest and most primitive tetrapods.

133. Säve-Söderbergh, G. 1932. "Preliminary Note on Devonian Stegocephalians from East Greenland," *Meddel. om Grønland*, Vol. **94**, No. 7. Pp. 107.
See comment in Westoll, No. 129.

134. Bystrow, A. P. 1935. "Morphologische Untersuchungen der Deckknochen des Schädels der Wirbeltiere. I. Mitteilungen. Schädel der Stegocephalen," *Acta zool.*, **16:**65–141.
Many good figures of labyrinthodonts and diplocaulids.

135. Watson, D. M. S. 1919. "On *Seymouria*, the Most Primitive Known Reptile," *Proc. Zoöl. Soc. London*, 1918, pp. 267–301.

136. White, T. E. 1939. "Osteology of *Seymouria baylorensis*," *Bull. Mus. Comp. Zoöl.*, **85:** 325–402.

137. Bystrow, A. P. 1944. "*Kotlassia prima* Amalitzky," *Bull. Geol. Soc. Amer.*, **55:**379–416.

138. Romer, A. S., and Witter, R. V. 1942. "*Edops*, a Primitive Rhachitomous Amphibian from the Texas Red Beds," *Jour. Geol.*, **50:**925–60.

139. Sawin, H. J. 1941. "The Cranial Anatomy of *Eryops megacephalus*," *Bull. Mus. Comp. Zoöl.*, **88:** 407–63.

140. Romer, A. S. 1939. "Notes on Branchiosaurs," *Amer. Jour. Sci.*, **237:**748–61.

141. ———. 1930. "The Pennsylvanian Tetrapods of Linton, Ohio," *Bull. Amer. Mus. Nat. Hist.*, **59:**77–147.
This paper and the one following describe as "phyllospondyls" many small Carboniferous labyrinthodonts.

142. Steen, M. 1930. "The British Museum Collection of Amphibia from the Middle Coal Measures of Linton, Ohio," *Proc. Zoöl. Soc. London*, 1930, pp. 849–91.

143. Fritsch, A. 1879–1901. *Fauna der Gaskohle und der Kalksteine der Permformation Böhmens.* 4 vols. Prague. Pp. 492+154 pls.
Many colored plates of amphibians, particularly "branchiosaurs" and lepospondyls.

144. Credner, H. 1881–93. "Die Stegocephalen und Saurier aus dem Rothliegenden des Plauen'schen Grundes bei Dresden. I–X," *Zeitschr. d. deutsch. geol. Gesellsch.*, Vols. **33–35, 37–38, 42.** Pp. 345.
"Branchiosaurs," etc.

145. Olson, E. C. 1941. "The Family Trematopsidae," *Jour. Geol.*, **49:**149–76.

146. Steen, M. 1934. "The Amphibian Fauna from the South Joggins, Nova Scotia," *Proc. Zoöl. Soc. London*, 1934, pp. 465–504.
Small primitive rhachitomes.

147. Case, E. C. 1935. "Description of a Collection of Associated Skeletons of *Trimerorhachis*," *Contr. Mus. Pal. Univ. Michigan*, **4:**227–74.

148. Bystrow, A. P. 1938. "*Dvinosaurus* als neotenische Form der Stegocephalen," *Acta zoöl.*, **19:**209–95.

149. Bystrow, A. P., and Efremov, J. A. 1940. "*Benthosuchus sushkini* Efr.—a Labyrinthodont from the Eotriassic of Sharjenga River," *Trav. Inst. Pal. Acad. Sci. U.R.S.S.*, Vol. **10.** Pp. 152.
Structure of a "neorhachitome."

150. Fraas, E. 1889. "Die Labyrinthodonten der schwäbischen Trias," *Palaeontogr.*, **36:** 1–158.

151. Nilsson, T. 1937. "Ein Plagiosauride aus dem Rhät Schonens," *Meddel. Lunds Geol.-Min. Inst.*, No. 72. Pp. 75.

—On *Micropholis* and *Lydekkerina* see Broili and Schroeder, No. 280, Parts XXV, XXVI; on late Carboniferous labyrinthodonts see Steen, No. 152.

LEPOSPONDYLS

152. Steen, M. 1938. "On the Fossil Amphibia from the Gas Coal of Nýřany and Other Deposits in Czechoslovakia," *Proc. Zoöl. Soc. London*, B, **108:**205–83.

Lepospondyls and labyrinthodonts.

153. Douthitt, H. 1917. "The Structure and Relationships of *Diplocaulus*," *Contr. Walker Mus.*, **2,** 1–40.

154. Sollas, W. J. 1920. "On the Structure of *Lysorophus* as Exposed by Serial Sections," *Phil. Trans. Roy. Soc. London*, B, **209:**481–527.

—Many figures in Fritsch, No. 143, and Steen, No. 142.

FROGS

155. Watson, D. M. S. 1941. "The Origin of Frogs," *Trans. Roy. Soc. Edinburgh*, **60:**195–231.

156. Piveteau, J. 1937. "Un Amphibien du Trias inférieur; essai sur l'origine et l'évolution des amphibiens anoures," *Ann. pal.*, **26:**135–76.

URODELES

157. Herre, W. 1935. "Die Schwanzlurche der mitteleocänen (oberlutetischen) Braunkohle des Geiseltales und die Phylogenie der Urodelen unter Einschluss der fossilen Formen," *Zoologica*, **33:**1–85.

REPTILES

Owen in England and Leidy and Cope in America were the most prominent of earlier writers. Among later workers in the field may be mentioned Williston, Baur, Broili, Nopcsa, Stromer, Sushkin, Hartmann-Weinberg, Stromer, Swinton, Parrington, Peyer, Wiman, Broom (especially therapsids), Case (Permian and Triassic), Watson (especially therapsids), Seeley (pterosaurs and therapsids), Brown, Gilmore, Huene, Janensch, and Lull (especially dinosaurs).

158. Williston, S. W. 1925. *The Osteology of the Reptiles*. Ed. W. K. Gregory. Cambridge. Pp. 300.

A valuable account of the skeleton of fossil reptiles, followed by a systematic section.

159. Nopcsa, F. von. 1926. *Osteologia reptilium fossilium et recentium*. "Fossilium catalogus," Pars 27. Berlin. Pp. 391. Also *Supplement*. "Fossilium catalogus," Pars 50 (1931). Pp. 62.

Lists (with comments as to content) every paper of importance dealing with fossil reptiles and amphibians.

160. Kuhn, O. 1937. *Die fossilen Reptilien*. Berlin. Pp. 121.

161. Williston, W. S. 1914. *Water Reptiles of the Past and Present*. Chicago. Pp. 251.

Semipopular account of aquatic groups.

162. Owen, R. 1849–1884. *A History of British Fossil Reptiles*. Reprinted from publications of the Palaeontographical Society, etc., London.

Many excellent figures of Mesozoic reptiles—turtles, dinosaurs, marine reptiles, etc.

163. Huene, F. von. 1940. Die Saurier der Karroo-, Gondwana- und verwandten Ablagerungen in faunistischer, biologischer und phylogenetischer Hinsicht," *Neues Jahrb. Min., Geol. Pal.*, Beil.-Bd., Abt. B, **83:**246–347.

Lists and comments on many of the older reptilian faunas.

COTYLOSAURIA

The American forms have been mainly described by Cope, Broili, Case, and Williston. Pareiasaurs were first adequately described by Seeley; the South African forms have been revised by Haughton and Boonstra (No. 169).

164. Case, E. C. 1911. "A Revision of the Cotylosauria of North America," *Pub. Carnegie Inst. Washington*, No. 145. Pp. 122.
Particularly *Diadectes*.

165. Williston, S. W. 1911. "A New Family of Reptiles from the Permian of New Mexico," *Amer. Jour. Sci.*, 4th ser. **31**:378–98.
Limnoscelis. Further described in *ibid.*, **34**:457–68.

166. ———. 1917. "*Labidosaurus* Cope, a Lower Permian Cotylosaur Reptile from Texas," *Jour. Geol.*, **25**:309–21.

167. Price, L. I. 1935. "Notes on the Braincase of *Captorhinus*," *Proc. Boston Soc. Nat. Hist.*, **40**:377–86.

168. ———. 1937. "Two New Cotylosaurs from the Permian of Texas," *Proc. New England Zoöl. Club*, **16**:97–102.
Primitive cotylosaur skulls.

169. Haughton, S. H., and Boonstra, L. D. 1929–34. "Pareiasaurian Studies. I–XI," *Ann. South African Mus.*, Vols. **28**, **31**.

170. Watson, D. M. S. 1914. "*Procolophon trigoniceps*, a Cotylosaurian Reptile from South Africa," *Proc. Zoöl. Soc. London*, 1914, pp. 735–47.
See also Broili and Schroeder, No. 280, Part XXI.

171. Huene, F. von. 1939. "Ein neuer Procolophonide aus dem deutschen Buntsandstein," *Neues Jahrb. Min., Geol. Pal.*, Beil.-Bd., Abt. B, **81**:501–11.

172. Efremov, J. A. 1940. "Die Mesen-Fauna der permischen Reptilien," *Neues. Jahrb. Min., Geol. Pal.*, Beil.-Bd., Abt. B, **84**:379–466.
Including early procolophonids.

CHELONIA

Turtles are the commonest of fossils in many late Mesozoic and Tertiary deposits, and more papers have been published on this group than on any other reptilian order; most, however, are routine descriptions of remains of the shell. Hay and Gilmore have been prominent students of this group.

173. Hay, O. P. 1908. "The Fossil Turtles of North America," *Pub. Carnegie Inst. Washington*, No. 75. Pp. 568.

174. Wieland, G. R. 1909. "Revision of the Protostegidae," *Amer. Jour. Sci.*, 4th ser., **27**:101–30.
Structure of *Archelon*, a Cretaceous marine turtle.

175. Jaekel, O. 1914–16. "Die Wirbeltierfunde aus dem Keuper von Halberstadt," *Pal. Zeitschr.*, **1**:155–215; **2**:88–214.
Describes *Triassochelys*, a primitive Triassic form.

176. Nopcsa, F. 1923. "*Kallokibotium*, a Primitive Amphichelydean Tortoise from the Uppermost Cretaceous of Hungary," *Pal. Hungar.*, **1**:1–34.

177. Watson, D. M. S. 1914. "*Eunotosaurus africanus* Seeley and the Ancestry of the Chelonia," *Proc. Zoöl. Soc. London*, 1914, pp. 1011–20.

178. Bergounioux, F. M. 1935. "Contribution à l'étude paléontologique des chéloniens: chéloniens fossiles du Bassin d'Aquitaine," *Mém. Soc. géol. France*, new ser., Vol. 11, Mém. 25. Pp. 215.

ICHTHYOSAURS

Ichthyosaurs were among the first of fossil reptiles to be discovered and described by early writers, such as Conybeare and Mantell. The typical Jurassic forms have been comprehensively reviewed by Huene (No. 179). Triassic types have been studied by Merriam and Wiman.

179. Huene, F. von. 1922. *Die Ichthyosaurier des Lias und ihre Zusammenhänge.* Berlin. Pp. 114+22 pls.
With a general discussion of ichthyosaur evolution and a bibliography.

180. Gilmore, C. W. 1905. "Osteology of *Baptanodon* Marsh," *Mem. Carnegie Mus.*, **2**:77–129, 325–37.
A good account of the same form (*Ophthalmosaurus*) in Andrews, No. 193.

181. Merriam, J. C. 1908. "Triassic Ichthyosauria with Special Reference to the American Forms," *Mem. Univ. California*, Vol. **1**. Pp. 196.

182. Wiman, C. 1910. Ichthyosaurier aus der Trias Spitzbergens," *Bull. Geol. Inst. Univ. Upsala*, **10**:124–48.
See also *ibid.*, **11**:230–41 (1912).

MESOSAURS

183. McGregor, J. H. 1908. *On* Mesosaurus brasiliensis, *nov. sp. from the Permian of Brazil.* Commisão de Estudos das Minas de Carvão de Pedra do Brazil. Pp. 302–36+4 pls.
A new skull reconstruction in Huene, No. 163.

PROTOROSAURIA

184. Williston, S. W. 1914. "The Osteology of Some American Permian Vertebrates," *Jour. Geol.*, **22**:364–419.
On *Araeoscelis*, with an argument for its relationship to the lizards.

185. Huene, F. von. 1926. "Zur Beurteilung von *Protorosaurus*," *Centralbl. Min., Geol. Pal.* Abt. B., 1926, pp. 469–75.

186. Peyer, B. 1931–37. "Die Triasfauna der Tessiner Kalkalpen. I–XII," *Abh. schweiz. Pal. Gesellsch.*, Vols. **50–59.**
Tanystropheus in Part II; *Macrocnemus* in Part XII; also treats of placodonts and nothosaurs.

187. Gregory, J. T. 1945. "Osteology and Relationships of *Trilophosaurus*," *Univ. Texas Publications* (in press).

188. Broili, F. 1926. "Ein neuer Fund von *Pleurosaurus* aus dem Malm Frankens," *Abh. bayer. Akad. Wiss., math.-nat. Abt.*, Vol. **30**, No. 8. Pp. 48.

SAUROPTERYGIANS

On Nothosaurs see Peyer, No. 186, Parts III–V, VII, IX.

On Plesiosaurs:

189. Williston, S. W. 1903. "North American Plesiosaurs. I," *Pub. Field Mus. Dept. Geol.*, **2**:1–77 (continued in *Amer. Jour. Sci.*, 4th ser., **21**:221–36 [1906]; *Proc. U.S. Nat. Mus.*, **32**:477–89 [1907]; and *Jour. Geol.*, **16**:715–36 [1908]).

190. Fraas, E. 1910. "Plesiosaurier aus dem oberen Lias von Holzmaden," *Palaeontogr.*, **57**:105–40.
Figures of two fine skeletons.

191. White, T. E. 1940. "Holotype of *Plesiosaurus longirostris* Blake and Classification of the Plesiosaurs," *Jour. Pal.*, **14**:451–67.

192. Welles, S. P. 1943. "Elasmosaurid Plesiosaurs with Description of New Material from California and Colorado," *Mem. Univ. California*, **13**:125–254.

193. Andrews, C. W. 1910–13. *A Descriptive Catalogue of the Marine Reptiles of the Oxford Clay.* 2 vols. London. Pp. 411+23 pls.

Plesiosaurs, crocodilians, ichthyosaurs. Good figures.

194. Edinger, T. 1935. "*Pistosaurus,*" *Neues Jahrb. Min., Geol. Pal.,* Beil.-Bd., **74**:321–59.

On placodonts:

195. Broili, F. 1912. "Zur Osteologie des Schädels von *Placodus,*" *Palaeontogr.,* **59**:147–55.

Good figures.

196. Drevermann, F. 1933. "Das Skelett von *Placodus gigas* im Senckenberg-Museum," *Abh. Senck. nat. Gesellsch.,* **38**:319–64.

Followed by a discussion by Huene, pp. 365–82.

197. Huene, F. von. 1936. "*Henodus chelyops,* ein neuer Placodontier," *Palaeontogr.,* Abt. A, **84**:99–148.

Further description in *ibid.,* Abt. A, **89**:105–14 (1938). See also Peyer, No. 186, Parts III and VIII.

EOSUCHIA

198. Broom, R. 1914. "A New Thecodont Reptile," *Proc. Zoöl. Soc. London,* 1914, pp. 1072–77; see also *Bull. Amer. Mus. Nat. Hist.,* **51**:67–76.

On *Youngina.*

199. ———. 1925. "On the Origin of Lizards," *Proc. Zoöl. Soc. London,* 1925. Pp. 16.

200. Olson, E. C. 1936. "Notes on the Skull of *Youngina capensis* Broom," *Jour. Geol.,* **44**: 523–33.

201. Parrington, F. R. 1935. "On *Prolacerta broomi,* gen. et sp. n., and the Origin of Lizards," *Ann. Mag. Nat. Hist.,* 10th ser., **16**:197–205.

202. Camp, C. L. 1945. "*Prolacerta* and the Protorosaurian Reptiles," *Amer. Jour. Sci.,* **243**: 18–32, 84–101.

203. Merriam, J. C. 1905. "The Thalattosauria, a Group of Marine Reptiles from the Triassic of California," *Mem. California Acad. Sci.,* Vol. **5**, No. 1. Pp. 52.

204. Brown, B. 1905. "The Osteology of *Champsosaurus* Cope," *Mem. Amer. Mus. Nat. Hist.,* **9**:1–26.

RHYNCHOCEPHALIA

205. Huene, F. von. 1929. "Ueber Rhynchosaurier und andere Reptilien aus den Gondwana-Ablagerungen Südamerikas," *Geol. u. pal. Abh.,* Vol. **21**. Pp. 62+8 pls.

Scaphonyx, a rhynchosaur, with a résumé of the Triassic rhynchocephalians. The *Scaphonyx* material is in process of revision; for later descriptions of rhynchosaurs see the following two papers.

206. ———. 1939. "Die Verwandtschaftsgeschichte der Rhynchosauriden," *Physis,* **14**:499–522.

207. ———. 1938. "*Stenaulorhynchus,* ein Rhynchosauride der ostafrikanischen Obertrias," *Nova acta Leopold.,* new ser., **6**:83–121.

SQUAMATA

On lizards:

208. Fejérváry, G. J. de. 1918. "Contributions to a Monography on Fossil Varanidae and on Megalanidae," *Ann. Mus. nat. hungar.,* **16**:341–467.

Additions in *ibid.,* Vol. **29**. Pp. 130.

209. Gilmore, C. W. 1928. "Fossil Lizards of North America," *Mem. Nat. Acad. Sci.,* **22**:1–201.

210. ———. 1943. "Fossil Lizards of Mongolia," *Bull. Amer. Mus. Nat. Hist.,* **81**:361–84.

On mosasaurs:

211. Williston, S. W. 1898. "Mosasaurs," *Univ. Geol. Surv. Kansas,* **4**:83–221.

212. Osborn, H. F. 1899. "A Complete Mosasaur Skeleton, Osseous and Cartilaginous," *Mem. Amer. Mus. Nat. Hist.*, **1**:167–88.

On snakes:

213. Gilmore, C. W. 1938. "Fossil Snakes of North America," *Geol. Soc. Amer., Spec. Papers*, No. 9. Pp. 96.

214. Simpson, G. G. 1933. "A New Fossil Snake from the *Notostylops* Beds of Patagonia," *Bull. Amer. Mus. Nat. Hist.*, **67**:1–22.

215. Hoffstetter, R. 1939. "Contribution à l'étude des élapidés actuels et fossiles et de l'ostéologie des ophidiens," *Arch. Mus. hist. nat. Lyon*, Vol. **15**. Pp. 82.

216. Nopcsa, F. 1923. "*Eidolosaurus* und *Pachyophis:* Zwei neue Neocom-Reptilien," *Palaeontogr.*, **65**:96–154.

THECODONTIA

Huene has worked most extensively on European forms; Broom and Haughton, on those of South Africa; Camp, Case, and Mehl have been active workers on the American phytosaurs.

216*a*. Huene, F. von. 1936. "The Constitution of the Thecodontia," *Amer. Jour. Sci.*, 5th ser. **32**:207–17.

217. Broom, R. 1913. "On the South African Pseudosuchian *Euparkeria* and Allied Genera," *Proc. Zoöl. Soc. London*, 1913, pp. 613–33.

Skulls, etc., of some generalized thecodonts. On *Chasmatosaurus* see Broili and Schroeder, No. 280, Part V.

218. Huene, F. von. 1921. "Neue Pseudosuchier und Coelurosaurier aus dem württembergischen Keuper," *Acta zool.*, **2**:329–403.

219. Haughton, S. H. 1924. "The Fauna and Stratigraphy of the Stormberg Series," *Ann. South African Mus.*, **12**:323–497.

Particularly *Sphenosuchus* and *Notochampsa.*

220. Huene, F. von. 1920. "Osteologie von *Aëtosaurus ferratus* O. Fraas," *Acta zool.*, **1**:465–91.

221. McGregor, J. H. 1906. "The Phytosauria, with Especial Reference to *Mystriosuchus* and *Rhytidodon*," *Mem. Amer. Mus. Nat. Hist.*, **9**:29–101.

222. Camp, C. L. 1930. "A Study of the Phytosaurs with Description of New Material from Western North America," *Mem. Univ. California*, **10**:1–161.

CROCODILIA

Mook has done much recent work on this group.

223. Mook, C. C. 1934. "The Evolution and Classification of the Crocodilia," *Jour. Geol.*, **42**:295–304.

224. ———. 1925. "A Revision of the Mesozoic Crocodilia of North America," *Bull. Amer. Mus. Nat. Hist.*, **51**:319–432; 2 pls.

225. Fraas, E. 1902. "Die Meer-Krokodilier (Thalattosuchia) des oberen Jura unter specieller Berücksichtigung von *Dacosaurus* und *Geosaurus*," *Palaeontogr.*, **49**:1–72.

226. Simpson, G. G. 1937. "New Reptiles from the Eocene of South America," *Amer. Mus. Novit.*, No. 927. Pp. 3.

Sebecus. Figured in Brown and Schlaikjer, No. 261.

—See also Andrews, No. 193, for Jurassic forms.

PTEROSAURIA

Seeley in England and Plieninger in Germany were among the more important workers on European Jurassic pterosaurs. The American Cretaceous forms were described mainly by Marsh and Williston.

227. Plieninger, F. 1930. *Pterosauria.* "Fossilium catalogus," Pars 45. Berlin. Pp. 84. Bibliography.

228. Seeley, H. G. 1901. *Dragons of the Air.* London. Pp. 240.
A good summary of older work, but illustrations none too good.

229. Plieninger, F. 1901. "Beiträge zur Kenntniss der Flugsaurier," *Palaeontogr.*, **48**: 65–90. *Pterodactylus*, etc.

230. Eaton, G. F. 1910. "Osteology of *Pteranodon*," *Mem. Connecticut Acad. Sci.*, **2**: 1–38.
A good account of this large form.

231. Stromer, E. 1913. "Rekonstruktionen des Flugsauriers *Rhamphorhynchus*," *Neues Jahrb. Min., Geol. Pal.*, **2**: 49–68.

232. Broili, F. 1936. "Weitere Beobachtungen an *Ctenochasma*," *Sitz.-Ber. bayer. Akad. Wiss. München*, 1936, pp. 137–56.

233. ———. 1938. "Beobachtungen an *Pterodactylus*," *ibid.*, 1938, pp. 139–54.

DINOSAURS, GENERAL

Many of the older European remains were described by Owen. In America, Marsh was the principal student of dinosaurs during the latter part of the nineteenth century. More recent workers on dinosaurs include Huene (particularly saurischians) and Nopcsa (especially ornithischians) in Europe; and Brown, Gilmore, Lull, Lambe, Parks, and C. M. Sternberg in North America. East African (Tendaguru) types have been described by Janensch and Hennig; Huene has discussed South American forms. For an elementary account of dinosaurs see Lull, No. 3. Restorations of a number of forms in Heilmann, No. 266.

234. Swinton, W. E. 1934. *The Dinosaurs: A Short History of a Great Group of Extinct Reptiles.* London. Pp. 233.

235. Matthew, W. D. 1915. "Dinosaurs," *Amer. Mus. Nat. Hist. Handbook*, No. 5. Pp. 117.
A popular account.

236. Marsh, O. C. 1896. The Dinosaurs of North America," *Sixteenth Ann. Rept. U.S. Geol. Surv.*, pp. 133–244.
Summarizes all of American types known to that date. Still valuable.

SAURISCHIA—BIPEDS

237. Huene, F. von. 1932. "Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte," *Mono. Geol. Pal.*, 1st ser., **4**: 1–368.
A modern summary of our knowledge of saurischian dinosaurs, with special reference to Triassic forms.

238. Lull, R. S. 1915. "Triassic Life of the Connecticut Valley," *Bull. Geol. and Nat. Hist. Surv. Connecticut*, **24**: 1–285.
Footprints of early dinosaurs, etc.

239. Huene, F. von. 1926. "The Carnivorous Saurischia in the Jura and Cretaceous Formations, Principally in Europe," *Rev. Mus. La Plata*, **29**: 35–167.
Review of knowledge of theropods (in broad sense) to 1921; particularly discusses "*Megalosaurus*" of European Jurassic and Lower Cretaceous and *Compsognathus.*

240. Gilmore, C. W. 1920. "Osteology of the Carnivorous Dinosauria in the United States National Museum, with Special Reference to the Genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*," *Bull. U.S. Nat. Mus.*, **110**: 1–159.

241. Osborn, H. F. 1917. "Skeletal Adaptations of *Ornitholestes, Struthiomimus, Tyrannosaurus*," *Bull. Amer. Mus. Nat. Hist.*, **35**: 733–71.
A well-illustrated account of these forms.

242. Lambe, L. M. 1917. The Cretaceous Theropodous Dinosaur *Gorgosaurus*," *Mem. Geol. Surv. Canada*, **100:** 1–84.

Osteology of a large Cretaceous carnivore.

243. Parks, W. A. 1928. "*Struthiomimus samueli*, a New Species of Ornithomimidae from the Belly River Formation of Alberta," *Univ. Toronto Studies, Geol. Ser.*, **26:** 1–24.

SAUROPODS

244. Huene, F. von. 1927. "Short Review of the Present Knowledge of the Sauropoda," *Mem. Queensland Mus.* **9:** 121–26; also in *Eclog. Geol. Helvet.*, Vol. 20 (1927).

245. Gilmore, C. W. 1925. "A Nearly Complete Articulated Skeleton of *Camarasaurus*, a Saurischian Dinosaur from the Dinosaur National Monument, Utah," *Mem. Carnegie Mus.*, **10:** 347–84.

246. Hatcher, J. B. 1901. "*Diplodocus* (Marsh), Its Osteology, Taxonomy and Probable Habits, with a Restoration of the Skeleton," *Mem. Carnegie Mus.*, **1:** 1–63.

See also Holland, *Mem. Carnegie Mus.*, **2:** 225–64 (1906) and **9:** 379–403 (1924).

247. Gilmore, C. W. 1936. "Osteology of *Apatosaurus* with Special Reference to Specimens in the Carnegie Museum," *Mem. Carnegie Mus.*, **11:** 175–300.

248. Janensch, W. 1935. "Die Schädel der Sauropoden *Brachiosaurus, Barosaurus* und *Dicraeosaurus* aus den Tendaguru-Schichten Deutsch-Ostafrikas," *Palaeontogr.*, Suppl. 7, Reihe 1, Teil II, pp. 147–248.

—See also Huene, No. 237.

ORNITHOPODS

249. Swinton, W. E. 1936. "Notes on the Osteology of *Hypsilophodon* and on the Family Hypsilophodontidae," *Proc. Zoöl. Soc. London*, 1936, pp. 555–78.

250. Gilmore, C. W. 1909. "Osteology of the Jurassic Reptile *Camptosaurus*," *Proc. U.S. Nat. Mus.*, **36:** 197–332.

251. Hooley, R. W. 1925. "On the Skeleton of *Iguanodon atherfieldensis*. sp. nov.," *Quart. Jour. Geol. Soc. London*, **81:** 1–60.

252. Lull, R. S., and Wright, N. E. 1942. "Hadrosaurian Dinosaurs of North America," *Geol. Soc. Amer., Spec. Papers*, No. 40. Pp. 242.

253. Brown, B., and Schlaikjer, E. M. 1943. "A Study of the Troödont Dinosaurs with the Description of a New Genus and Four New Species," *Bull. Amer. Mus. Nat. Hist.*, **82:** 121–49.

STEGOSAURS

254. Gilmore, C. W. 1914. "Osteology of the Armored Dinosauria in the United States National Museum, with Special Reference to the Genus *Stegosaurus*," *Bull. U.S. Nat. Mus.*, **89:** 1–143.

255. Hennig, E. 1925. "*Kentrurosaurus aethiopicus:* Die Stegosaurier-Funde vom Tendaguru, Deutsch-Ostafrika," *Palaeontogr.*, Suppl. 7, Reihe I, Teil I, pp. 101–254.

255*a*. Janensch, W. 1925. "Ein aufgestelltes Skelett des Stegosauriers *Kentrurosaurus aethiopicus* E. Hennig aus den Tendaguru-Schichten Deutsch-Ostafrikas," *Palaeontogr.*, Suppl. 7, Reihe I, Teil I, pp. 255–76.

Description of an East African form related to *Stegosaurus*.

ANKYLOSAURS

256. Lull, R. S. 1921. "The Cretaceous Armored Dinosaur *Nodosaurus textilis* Marsh," *Amer. Jour. Sci.*, 5th ser., **1:** 97–126.

257. Nopcsa, F. 1929. "Dinosaurierreste aus Siebenbürgen," *Geol. Hungar. ser. pal. Fasc.* **4:** 1–72.

258. Sternberg, C. M. 1928. "A New Armored Dinosaur from the Edmonton Formation of Alberta," *Trans. Roy. Soc. Canada*, 3d ser., **22**:93–106.

HORNED DINOSAURS

259. Hatcher, J. B.; Marsh, O. C.; and Lull, R. S. "The Ceratopsia," *Mono. U.S. Geol. Surv.*, **49**:1–157.
Includes all the earlier work.

260. Lull, R. S. 1933. "A Revision of the Ceratopsia or Horned Dinosaurs," *Mem. Peabody Mus. Nat. Hist.*, Vol. **3**, Part III. Pp. 135.

261. Brown, B., and Schlaikjer, E. M. 1940. "The Structure and Relationships of *Protoceratops*," *Ann. New York Acad. Sci.*, **40**:133–266.

BIRDS

The literature on fossil birds is widely scattered. Wetmore, Miller, and Howard in America and the late K. Lambrecht of Budapest have been the more recent active workers.

262. Lambrecht, K. 1933. *Handbuch der Palaeornithologie*. Berlin. Pp. 1024.
A well-documented account.

263. Pycraft, W. P. 1910. *A History of Birds*. London. Pp. 489+37 pls.
A general account, with some mention of fossil forms.

264. Wetmore, A. 1929. "Birds of the Past in North America," *Smithsonian Inst. Washington Rept.*, 1928, pp. 337–89.

265. ———. 1940. A Check-List of the Fossil Birds of North America. *Smithsonian Misc. Coll.*, Vol. **99**. No. 4. Pp. 81.

266. Heilmann, G. 1926. *The Origin of Birds*. London. Pp. 208+2 pls.
A well-illustrated and readable discussion of bird origins, with an account of Jurassic and Cretaceous birds, the reconstruction of a hypothetical "Proavis," and a résumé of the archosaurian reptile groups.

267. Marsh, O. C. 1880. "Odontornithes: A Monograph on the Extinct Toothed Birds of North America," *Rept. Geol. Expl. 40th Parallel*. Pp. 201.

268. Milne-Edwards, A. 1867–71. *Récherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France*. 2 vols text; 2 vols. pls. Paris.
Tertiary fossil types and numerous illustrations of skeletons of modern forms as well.

269. Matthew, W. D., and Granger, W. 1917. "The Skeleton of *Diatryma*, a Gigantic Bird from the Lower Eocene of Wyoming," *Bull. Amer. Mus. Nat. Hist.*, **37**:307–326.

270. Owen, R. 1879. *Memoirs on the Extinct Wingless Birds of New Zealand*. London. Pp. 513+123 pls.
Moas, etc. Mainly a reprint of the author's previous separate papers on these forms.

271. Miller, L. H. 1925. "The Birds of Rancho La Brea," *Pub. Carnegie Inst. Washington*, **349**:63–106.

272. Howard, H. 1927. "A Review of the Fossil Bird, *Parapavo californicus* (Miller), from the Pleistocene Asphalt Beds of Rancho La Brea," *Univ. California Pub., Bull. Dept. Geol. Sci.*, **17**:1–62.

273. ———. 1932. "Eagles and Eagle-like Vultures of the Pleistocene of Rancho La Brea," *Pub. Carnegie Inst. Washington*, No. 429, 1–82.

274. Wiman, C., and Edinger, T. 1942. "Sur les crânes et les encéphales d'*Aepyornis* et de *Mullerornis*," *Bull. Acad. Malgache*, Vol. **24**. Pp. 50.

275. Lydekker, R. 1891. *Catalogue of Fossil Birds in the British Museum*. London. Pp. 368.

276. Gaillard, C. 1939. "Contribution à l'étude des oiseaux fossiles," *Arch. Mus. hist. nat. Lyon*, Vol. **15**. Pp. 100.

276a. Simpson, G. G. 1945. "Fossil Penguins," *Bull. Amer. Mus. Nat. Hist.* (in press).

PELYCOSAURS

The earlier work on these forms was done principally by Cope, Case, and Williston; Broom, Watson, and Huene have also contributed.

277. Romer, A. S., and Price, L. I. 1940. "Review of the Pelycosauria," *Geol. Soc. Amer., Spec. Papers*, No. 28. Pp. 538.

THERAPSIDA

The South African mammal-like forms were first studied by Owen, later by Seeley. Work by Broom during the last four decades has been instrumental in showing the importance and diversity of these forms. Watson has contributed a number of important papers on morphology; Haughton, Boonstra, Broili and Schroeder, Parrington, and Olson have contributed morphological and systematic studies. New Russian therapsids are in process of description by Bystrow.

278. Broom, R. 1932. *The Mammal-like Reptiles of South Africa and the Origin of Mammals.* London. Pp. 376.

An important comprehensive account. Numerous further papers by this writer in recent volumes of *Ann. Transvaal Mus.*

279. Parrington, F. R., and Westoll, T. S. 1940. "On the Evolution of the Mammalian Palate," *Phil. Trans. Roy. Soc. London*, B, **230**:305–55.

280. Broili, F., and Schroeder, J. 1934–37. "Beobachtungen an Wirbeltieren der Karrooformation. I–XXVIII," *Sitz.-Ber. bayer. Akad. Wiss. München*, 1934–37.

Good description of *Cynognathus* and other cynodonts, gorgonopsians, therocephalians, bauriamorphs, dicynodonts, and dinocephalians; also *Chasmatosaurus*, *Procolophon*, *Tritylodon*, and labyrinthodonts.

281. Broom, R. 1929. "On the Carnivorous Mammal-like Reptiles of the Family Titanosuchidae," *Ann. Transvaal Mus.*, **13**:9–36.

282. Efremov, J. A. 1940. "Preliminary Description of the New Permian and Triassic Tetrapoda from U.S.S.R.," *Trav. Inst. Pal. Acad. Sci. U.R.S.S.*, Vol. 10, Part II. Pp. 156.

Particularly primitive dinocephalians.

283. ———. 1940. "*Ulemosaurus svijagensis* Riab.—ein Dinocephale aus den Ablagerungen des Perm der UdSSR," *Nova acta Leopold.*, new ser., **9**:155–205.

284. Olson, E. C. 1944. "Origin of Mammals Based upon Cranial Morphology of the Therapsid Suborders," *Geol. Soc. Amer., Spec. Papers*, No. 55. Pp. 136.

285. Watson, D. M. S. 1921. "The Bases of Classification of the Theriodontia," *Proc. Zoöl. Soc. London*, 1921, pp. 35–98.

286. Broom, R. 1930. "On the Structure of the Mammal-like Reptiles of the Sub-order Gorgonopsia," *Phil. Trans. Roy. Soc. London*, B, **218**:345–71.

287. Boonstra, L. D. 1934. "A Contribution to the Morphology of the Gorgonopsia; Additions to Our Knowledge of the South African Gorgonopsia, Preserved in the British Museum (Natural History); A Contribution to the Morphology of the Mammal-like Reptiles of the Sub-order Therocephalia," *Ann. South African Mus.*, **31**:137–267.

288. Broom, R. 1936. "On the Structure of the Skull in the Mammal-like Reptiles of the Suborder Therocephalia," *Phil. Trans. Roy. Soc. London*, B, **226**:1–42.

289. Watson, D. M. S. 1931. "On the Skeleton of a Bauriamorph Reptile," *Proc. Zoöl. Soc. London*, 1931, pp. 1163–1205.

ICTIDOSAURIA

Some data on these problematical forms in Simpson, No. 346, pp. 11–30, 49–67; Broom, No. 278, pp. 299–307. On *Tritylodon* see also Broili and Schroeder, No. 280, Part XIX.

290. Simpson, G. G. 1926. "*Dromatherium* and *Microconodon*," *Amer. Jour. Sci.*, 5th ser., **12**: 89–108.

291. Young, C. C. 1940. "Preliminary Notes on the Mesozoic Mammals of Lufeng, Yunnan," *Bull. Geol. Soc. China*, **20**:93–111.
On the tritylodontid *Bienotherium*.

292. Watson, D. M. S. 1942. "On Permian and Triassic Tetrapods," *Geol. Mag.*, **79**:81–116.
On the *Tritylodon* group, etc.

MAMMALS, GENERAL

Cuvier and Owen were early European students of fossil mammals, followed later by such workers as Gaudry, Gervais, and Filhol in France; Forsyth Major and Lydekker in England; Kowalevsky and Rütimeyer in Central Europe. Among recent or active European students of mammals may be cited Abel, Airaghi, Andrée, Andrews, Bachofen-Echt, Bate, Berckhemer, Bohlin, Borissiak, Boule, Dal Piaz, Depéret, Dietrich, Ehrenberg, D'Erasmo, Forster-Cooper, Frentzen, Gaillard, Gromova, Haupt, Helbing, Heller, Hopwood, Hürzeler, Kormos, Kubacska, Leonardi, De Lorenzo, Mottl, Orlov, Patané, Paucă, Pilgrim, Revilliod, Reynolds, Roman, Schaub, Schlosser, Sickenberg, Simionescu, Slodkewitsch, Soergel, Stehlin, Stromer, Teilhard de Chardin, Tobien, Van der Vlerk, Viret, Welwlé, Weitzel, Zdansky, and Želízko. Indian material was described in earlier times by Falconer and Lydekker, more recently by Pilgrim, Forster-Cooper, Matthew, and Colbert. Much Chinese mammal material has been described by a series of writers in *Palaeontologia Sinica* on the basis of material collected by Swedish expeditions. Mongolian mammals have been collected by the American Museum (New York), and numerous papers have been published by Matthew and Granger. In recent years Young and other native writers have begun important contributions to the literature of paleontology in China. The important Fayûm, Egypt, fauna has been described mainly by Andrews and Schlosser.

In America all of the three principal early workers—Leidy, Cope, and Marsh—published voluminously on mammals. Leidy's and Cope's major works are cited below (Nos. 306–8), while Cope published numerous smaller papers in the *American Naturalist* and Marsh's many publications are scattered through the *American Journal of Science*. Osborn, Scott, Wortman, Matthew, Barbour, Gregory, Granger, Loomis, Merriam, Peterson, and Sinclair were later entrants into the field. Younger workers now active include: Bode, Burke, Chaffee, Clarke, Colbert, Cook, Denison, Dice, Falkenbach, Gazin, J. T. Gregory, Hesse, Hibbard, Jepsen, Kellogg, Lewis, McGrew, Meade, Patterson, Schlaikjer, C. B. Schultz, J. R. Schultz, Simpson, Skinner, Stirton, Stock, Stovall, Strain, Thorpe, Troxell, VanderHoof, T. E. White, L. E. Wilson, R. W. Wilson, A. E. Wood, and H. E. Wood.

Much of the important South American fossil mammal material was described by Florentino Ameghino on the basis of material collected by his brother Carlos; much of the importance of this work, however, was obscured by the erection by Ameghino of an impossible phylogenetic hypothesis in which, patriotically, South America was made a great center of general mammalian evolution. A number of types, particularly from the Pleistocene, were described by Owen, Burmeister, Gaudry, Roth, Lydekker, and other early writers. The Santa Cruz (Miocene) forms have been monographed by Scott and Sinclair on the basis of material collected for Princeton by Hatcher; and Loomis has revised the *Pyrotherium* beds fauna. Early Tertiary material has been recently described by Simpson, and later Tertiary collections by Riggs have been described by him and by Patterson and Scott. Recent South American writers include Bordas, Cabrera, Castellanos, Kraglievich and Rusconi.

GENERAL

293. Weber, M.; Burlet, H. M. de; and Abel, O. 1928. *Die Säugetiere*. 2d ed. 2 vols. Jena.
A standard work on mammalian anatomy and classification. The treatment of fossils is uneven.

294. Flower, W. H., and Lydekker, R. 1891. *An Introduction to the Study of Mammals, Living and Extinct.* London. Pp. 763.

Still a good account of living forms, although much of the paleontology is out of date.

295. Gregory, W. K. 1910. "The Orders of Mammals," *Bull. Amer. Mus. Nat. Hist.*, **27**:1–524.

A basic work on classification.

296. Simpson, G. G. 1945. "The Principles of Classification and a Classification of Mammals," *Bull. Amer. Mus. Nat. Hist.* (in press).

Includes full generic lists with distribution in time and space.

297. Winge, H. 1941. *The Interrelationships of the Mammalian Genera,* Vol. I: *Monotremata, Marsupialia, Insectivora, Chiroptera, Edentata.* Translated from the Danish by E. Deichmann and G. M. Allen. Copenhagen. Pp. 418.

Winge's influential and stimulating, if unorthodox, views on mammalian phylogeny have hitherto been available only in Danish.

298. Flower, W. H. 1885. *An Introduction to the Osteology of the Mammalia.* 3d ed. London. Pp. 383.

An old, but very useful, little book.

299. Trouessart, E. L. 1897–99. *Catalogus mammalium tam viventium quam fossilium.* New ed. Berlin. Pp. 1469. Also *Supplement* (1904–5). Pp. 929.

300. Matthew, W. D. 1915. "Climate and Evolution," *Ann. New York Acad. Sci.*, **24**:171–318.

Important on geographic history of mammals. A new edition with notes was published in 1939.

301. Simpson, G. G. 1940. "Mammals and Land Bridges," *Jour. Washington Acad. Sci.*, **30**, No. 4, 137–63.

302. Osborn, H. F. 1910. *The Age of Mammals in Europe, Asia, and North America.* New York. Pp. 652.

A faunal treatment, somewhat out of date but still useful. The Pleistocene material was revised in *Ann. New York Acad. Sci.*, **26**:215–315 (1915).

303. Scott, W. B. 1937. *A History of Land Mammals in the Western Hemisphere.* 2d. ed. New York. Pp. 786.

A good semitechnical account of the more prominent groups of American fossils.

304. Blainville, H. M. D. 1839–64. *Osteographie des mammifères.* 4 vols. Paris.

An early comprehensive illustrated account of fossil mammals. Cuvier's still earlier work (No. 4) is mainly devoted to mammals also.

305. Gregory, W. K. 1934. "A Half Century of Trituberculy: The Cope-Osborn Theory of Dental Evolution, with a Revised Summary of Molar Evolution from Fish to Man," *Proc. Amer. Phil. Soc.*, **73**:169–317.

Molar tooth evolution.

306. Leidy, J. 1854. "The Ancient Fauna of Nebraska," *Smithsonian Contrib. Knowl.*, Vol. 6, Art. 7. Pp. 126.

This and the following contain the original descriptions of many American fossil types.

307. ———. 1869. "The Extinct Mammalian Fauna of Dakota and Nebraska, Including an Account of Some Allied Forms from Other Localities, Together with a Synopsis of the Mammalian Remains of North America," *Jour. Acad. Nat. Sci. Philadelphia,* 2d ser., Vol. 7. Pp. 472.

308. Cope, E. D. 1884. "The Vertebrata of the Tertiary Formations of the West," *Rept. U.S. Geol. Surv. Territ.*, Vol. 3. Pp. 1044.

"Cope's Bible," a huge tome, which figures and describes a great number of Tertiary mammals. A basic work of importance, although many of the forms included have been described later from more complete material.

309. Schlosser, M. 1887–90. "Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des europäischen Tertiärs," *Beitr. Pal. Geol. Oesterr.-Ungarns*, **6**: 1–227; **7**: 1–162; **8**: 1–107.

Valuable summary and index to the older material of smaller mammal types of Europe. Unfortunately, few illustrations.

FAUNAL AND REGIONAL PAPERS

310. Wood, H. E., and Others. 1941. "Nomenclature and Correlation of the North American Continental Tertiary," *Bull. Geol. Soc. Amer.*, Vol. **52**. Pp. 48.

Currently accepted arrangement of North American mammal-bearing beds.

311. Simpson, G. G. 1937. "The Beginning of the Age of Mammals," *Biol. Rev.*, **12**: 1–47.

Paleocene mammals reviewed.

312. Matthew, W. D. 1937. "Paleocene Faunas of the San Juan Basin, New Mexico," *Trans. Amer. Phil. Soc.*, new ser., **30**: 1–510. (Edited by Granger, Gregory, and Colbert.)

313. Simpson, G. G. 1937. "The Fort Union of the Crazy Mountain Field, Montana, and Its Mammalian Faunas," *Bull. U.S. Nat. Mus.* **169**: 1–287.

314. Gazin, C. L. 1941. "The Mammalian Faunas of the Paleocene of Central Utah, with Notes on the Geology," *Proc. U.S. Nat. Mus.*, **91**: 1–53.

315. Jepsen, G. L. 1940. "Paleocene Faunas of the Polecat Bench Formation, Park County, Wyoming. I," *Proc. Amer. Phil. Soc.*, **83**, No. 2, 217–340.

The first part (on multituberculates) of a projected monograph on Wyoming Paleocene mammals.

316. Matthew, W. D. 1927. "The Evolution of the Mammals in the Eocene," *Proc. Zoöl. Soc. London*, 1927, pp. 947–85.

A summary of probable relationships of placental groups and their early evolution.

317. Matthew, W. D., and Granger, W. 1915–18. "A Revision of the Lower Eocene Wasatch and Wind River Faunas. I–V," *Bull. Amer. Mus. Nat. Hist.*, **34**: 1–103, 311–28, 329–61, 429–83; **38**: 565–657.

318. Stehlin, H. G. 1903–16. "Die Säugetiere des schweizerischen Eocaens: Critischer Catalog der Materialien," *Abh. Schweiz. pal. Gesellsch.*, **30**: 1–153; **31**: 155–455; **32**: 447–595; **33**: 597–690; **35**: 691–837; **36**: 839–1164; **38**: 1165–1298; **41**: 1297–1552.

Mainly a detailed discussion of the dentition and its bearing on the relationships of European Eocene forms.

319. Filhol, H. 1876–77. "Recherches sur les phosphorites du Quercy: étude des fossiles qu'on y rencontre et spécialement des mammifères," *Ann. sci. géol.*, **7**: 1–220; **8**: 1–340. Also published as a separate work.

320. ———. 1882. Etude des mammifères fossiles de Ronzon (Haute-Loire)," *Ann. sci. géol.*, **12**: 1–271.

Oligocene European mammals.

321. Scott, W. B.; Jepsen, G. L.; and Wood, A. E. 1941. "The Mammalian Fauna of the White River Oligocene," *Trans. Amer. Phil. Soc.*, new ser., Vol. **28**. Pp. 980.

An excellent and well-illustrated discussion of American Oligocene mammals. A similar work on the Uinta fauna is in progress.

322. Matthew, W. D. 1901. "Fossil Mammals of the Tertiary of Northeastern Colorado," *Mem. Amer. Mus. Nat. Hist.*, **1**, Part VII, 353–446.

Oligocene and Miocene forms.

323. Peterson, O. A. 1906. "The Miocene Beds of Western Nebraska and Eastern Wyoming and Their Vertebrate Faunae," *Ann. Carnegie Mus.*, **4**, No. 1, 21–72.

324. Filhol, H. 1881. "Etude des mammifères fossiles de Saint-Gérand le Puy (Allier)," *Ann. sci. géol.*, **11**:1–86.
Lower Miocene mammals.

325. ———. 1891. "Etude sur les mammifères fossiles de Sansan," *ibid.*, **21**:1–319.
Middle Miocene.

326. Matthew, W. D. 1924. "Third Contribution to the Snake Creek Fauna," *Bull. Amer. Mus. Nat. Hist.*, **50**:59–210.
Late Miocene and early Pliocene.

327. ———. 1929. "Critical Observations upon Siwalik Mammals," *ibid.*, **56**:437–560.
Includes discussion of evolution of bears, cats, chalicotheres, and giraffes.

328. Colbert, E. H. 1935. "Siwalik Mammals in the American Museum of Natural History," *Trans. Amer. Phil. Soc.*, **26**:1–401.
A more recent monograph on the same subject as the last, with discussion of the evolution of many groups.

329. Gaudry, A. 1867. *Animaux fossiles et géologie de l'Attique.* 2 vols. Paris. Pp. 474.
A classic account of a Pontian (Pliocene) fauna.

330. Hopwood, A. T. 1929. "A Review of the Fossil Mammals of Central Africa," *Amer. Jour. Sci.*, 5th ser., **17**:101–18.

331. Boule, M. 1906. *Les Grottes de Grimaldi: géologie et paléontologie.* Monaco. Pp. 363.
A Pleistocene cave fauna.

332. Reynolds, S. H. 1902–39. "A Monograph of the British Pleistocene Mammalia," *Mono. Palaeontogr. Soc. London*, Vols. **2** and **3**.

333. Young, C. C. 1934. "On the Carnivora from Locality I of Choukoutien; on the Artiodactyla from the *Sinanthropus* Site; on the Insectivora, Chiroptera, Rodentia, and Primates Other than *Sinanthropus* from Locality I at Choukoutien," *Pal. Sinica*, Ser. C, Vol. **8**. Pp. 405.
Describes an abundant Pleistocene fauna from eastern Asia. For additional accounts of this fauna see Vol. **5**, Fasc. 4, and (new ser.). Nos. 5, 9, 10, of the same publication.

334. Hay, O. P. 1923–27. "The Pleistocene of North America and Its Vertebrated Animals," *Pub. Carnegie Inst. Washington*, Nos. 322, 322*A*, 322*B*. Pp. 1230.

335. Stock, C. 1930. "Rancho La Brea: A Record of Pleistocene Life in California," *Pub. Los Angeles Mus.*, No. 1. Pp. 82.

336. Romer, A. S. 1933. "Pleistocene Vertebrates and Their Bearing on the Problem of Human Antiquity in North America." In: Jenness, D., *The American Aborigines* (Toronto), pp. 49–83.

337. Koenigswald, G. H. R. von. 1933. "Beitrag zur Kenntnis der fossilen Wirbeltiere Javas," *Dienst Mijn. Ned.-Indië, Wet. Meded.*, Vol. **1**, No. 23. Pp. 178.
Pleistocene fauna of East Indies.

338. Boule, M., and Thévenin, A. 1920. *Mammifères fossiles de Tarija.* Paris. Pp. 255.
A South American Pleistocene fauna.

339. Andrews, R. C. 1932. *The New Conquest of Central Asia: A Narrative of the Central Asiatic Expeditions in Mongolia and China*, 1921–1930. New York. Pp. 678.
Includes data on vertebrate fossils.

340. Simpson, G. G. 1940. "Review of the Mammal-bearing Tertiary of South America," *Proc. Amer. Phil. Soc.*, **83**:649–709.

341. ———. 1942. "Early Cenozoic Mammals of South America," *Proc. 8th Amer. Sci. Cong.*, **4**:303–32.

342. Scott, W. B. 1942. "The Later Cenozoic Mammalian Faunas of South America," *Proc. 8th Amer. Sci. Cong.*, **4**, 333–5

343. Ameghino, F. 1889. "Contribución al conocimiento de los mamíferos fósiles de la República Argentina," *Actas Acad. nac. cienc., Córdoba,* **6**:1–1028.

Reprinted as Vols. **6–9** of *Obras completas y correspondencia científica de F. Ameghino* (La Plata). This and the following are two of Ameghino's basal contributions to the paleontology of South America.

344. ———. 1906. "Les Formations sédimentaires du Crétacé supérieur et du tertiaire de Patagonie," *An. Mus. nac. hist. nat. Buenos Aires,* 3d ser., Vol. **8**. Pp. 568.

Reprinted as Vol. **16** of *Obras completas.*

MESOZOIC ORDERS

345. Simpson, G. G. 1935. "The First Mammals," *Quart. Rev. Biol.,* **10**:154–80.

346. ———. 1928. *A Catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum.* London. Pp. 225+12 pls.

Except for a few recent finds, this and the following give a complete account of pre-Tertiary mammals.

347. ———. 1929. "American Mesozoic Mammalia," *Mem. Peabody Mus. Yale Univ.,* Vol. **3**, Part I. Pp. 235.

348. Granger, W., and Simpson, G. G. 1929. "A Revision of the Tertiary Multituberculata," *Bull. Amer. Mus. Nat. Hist.,* **56**, 601–76.

349. Simpson, G. G. 1937. "Skull Structure of the Multituberculata," *Bull. Amer. Mus. Nat. Hist.,* **73**, 727–63.

On multituberculates see also Jepsen, No. 315; Simpson, No. 313, pp. 80–104; Matthew, No. 312, pp. 277–96.

MARSUPIALS

350. ———. 1930. *Postmesozoic Marsupialia.* "Fossilium catalogus, I, Animalia," Pars 47. Berlin. Pp. 87.

Literature and a general discussion of marsupial evolution.

351. Sinclair, W. J. 1906. "Mammalia of the Santa Cruz Beds: Marsupialia," *Rept. Princeton Univ. Exped. Patagonia,* **4**:333–460; 26 pls.

352. Simpson, G. G. 1940. "The Development of Marsupials in South America," *Physis,* **14**: 373–98.

353. Owen, R. 1878. *Researches on the Fossil Remains of the Extinct Mammals of Australia.* London.

Reprints of papers previously published separately in *Phil. Trans. Roy. Soc. London* (1859–72); *Diprotodon, Thylacoleo,* and other Pleistocene forms.

—See also Simpson, No. 347; Filhol, No. 320, pp. 51–68; Scott, No. 321, pp. 960–63.

INSECTIVORES

354. Gregory, W. K., and Simpson, G. G. 1926. "Cretaceous Mammal Skulls from Mongolia," *Amer. Mus. Novit.,* No. 225. Pp. 20.

Description of the oldest-known placentals. Popular account by Gregory in *Scientific Monthly,* March, 1927, pp. 225–35; see also Simpson in *Amer. Mus. Novit.,* Nos. 329 and 330 (1928).

—See also Simpson, No. 345; Matthew, No. 316; Matthew, No. 312, pp. 209–28; Matthew and Granger, No. 317, Parts IV and V; Matthew, No. 374, pp. 502–49; Scott, No. 321, pp. 9–26; Simpson, No. 313, pp. 104–40; Filhol, No. 319, pp. 8–14.

BATS

355. Revilliod, P. 1917–22. "Contribution à l'étude des Chiroptères des terrains Tertiaires," *Mém. Soc. pal. Suisse,* **43**:1–57; **44**:63–128; **45**:133–95.

TAENIODONTS

See Matthew, No. 312, pp. 228–77.

TILLODONTS

356. **Marsh, O. C.** 1876. "Principal Characters of the Tillodontia," *Amer. Jour. Sci.*, 3d ser., **11**:249–52.

See also Cope, No. 308.

PRIMATES

Fossils are few, but the literature is vast. Gregory has been the most thorough student of primate evolution; workers on lower primates include Le Gros Clark, Jepsen, Lewis, and Simpson. Among students of human evolution may be mentioned: Du Bois and Koenigswald (*Pithecanthropus*); Black and Weidenreich (*Sinanthropus*); Smith Woodward (*Eoanthropus*) Boule, Keith, and Elliot Smith. On dental evolution see Gregory, No. 305.

357. Clark, W. E. Le Gros. 1934. *Early Forerunners of Man.* Baltimore. Pp. 296.

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INDEX

The index is mainly taxonomic. It includes references to all genera contained in the classification as well as the text, and to the more common popular names. Families are not, in general, listed but may be located by consulting the type genus. All taxonomic terms of higher rank are given.

A few of the more general accounts of major skeletal features have been indexed, and references are given to the place where various structures are first described or defined. For the details of anatomy in the various types, consult the name of the genus or group. Various geologic and geographic terms are included.

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